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**ECOLOGY OF A REESTABLISHED POPULATION OF MUSKOXEN IN
NORTHEASTERN ALASKA**

**A
Thesis**

**Presented to the Faculty of the University of Alaska
in Partial Fulfillment of the Requirements
for the Degree of**

DOCTOR OF PHILOSOPHY

**By
Patricia Claire Embry Reynolds, B.S. M.S.**

Fairbanks, Alaska

August 1998

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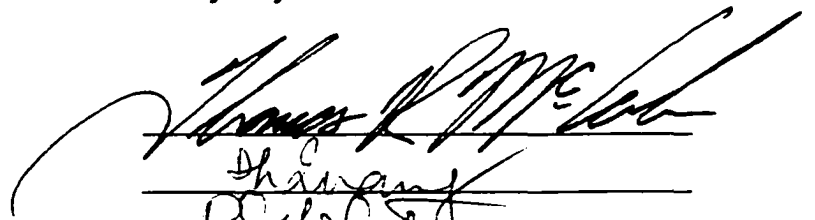
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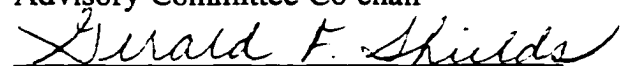
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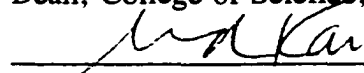
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ABSTRACT

The restoration of muskoxen (*Ovibos moschatus*) to regions of former range in northeastern Alaska presented an opportunity to study population dynamics, seasonal patterns, and dispersal in an expanding population of ungulates. Muskoxen were returned to the Arctic National Wildlife Refuge (Arctic NWR) in 1969-70 after an absence of >100 years. In 1982-97, I used annual censuses, counts by sex and age, radio and satellite telemetry, and data from Landsat-TM maps to determine rates of population growth, changes in production, survival, and group size over time, seasonal habitat use, activity patterns, and dispersal of mixed-sex groups. In 1982-86, mixed-sex groups of muskoxen occupied the same regions as in 1977-81, but annual rates of increase and calf production declined (1977-81: rate = 0.24, 87 calves/100 adult females; 1982-86: rate = 0.14, 61 calves/100 adult females). In 1987-95, numbers of muskoxen in regions first occupied declined and stabilized at <300 animals as calf production continued to decline and mixed-sex groups dispersed into unoccupied regions. Survival of calves and yearlings did not decline over time. By 1995, about 800 muskoxen were distributed between the Itkillik River west of Prudhoe Bay, Alaska, and the Babbage River in northwestern Canada. In summer, female muskoxen occupied large core areas ($\bar{x} = 223 \text{ km}^2$), and had high rates of movement ($\bar{x} = 2.6 \text{ km/day}$) and activity ($\bar{x} = 18.9 \text{ counts/min}$). In winter muskoxen remained in small core areas (mid-winter $\bar{x} = 25 \text{ km}^2$) and reduced movements (mid-winter $\bar{x} = 1.4 \text{ km/day}$) and activity (mid-winter $\bar{x} = 11.8 \text{ counts/min}$.) possibly as a strategy to conserve energy. Muskoxen selected (use > availability) riparian and moist sedge vegetation along rivers in all seasons. Dispersal of mixed-sex groups occurred infrequently through periodic pulses. Population density likely influenced patterns of dispersal through social interactions and habitat change. Weather conditions that affected the length of the growing season and availability of winter forage were major

factors in the dynamics, distribution, and dispersal patterns of this reestablished population of muskoxen.

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INTRODUCTION

Muskoxen (*Ovibos moschatus*) disappeared from Alaska before the turn of the 20th century during a period when other populations in Canada and Greenland were in decline. Concerns raised about possible worldwide extinction of the species prompted the United States government to reestablish the species in Alaska. Muskoxen captured in Greenland were released on Nunivak Island off the western Alaskan coast in 1935 and 1936. By the late 1960's, this population had grown to > 700 animals and surplus animals were available for translocation into regions of former range. During the next two decades, muskoxen from Nunivak Island were moved to several locations in Alaska: Nelson Island, northeastern Alaska, northwestern Alaska, and the Seward Peninsula. Muskoxen released at Barter Island and on the Kavik River in 1969 and 1970 were the source of the population that is the subject of this study.

The return of muskoxen to areas of former range in northeastern Alaska provided an opportunity to study the ecology of an expanding population of ungulates. Earlier studies of muskoxen in the Arctic National Wildlife Refuge (Arctic NWR) focused on habitat use relationships. My objectives were to investigate factors related to changes in abundance, distribution, activity and habitat use to understand the processes of population dynamics, range expansion and dispersal in this reestablished population.

Chapter 1 presents the results of research to determine the dynamics of the muskox population reestablished in northeastern Alaska. This study described changes in animal abundance and distribution over time and examined factors associated with these changes in regions that were first occupied by muskoxen after their release. I determined rates of population growth from animal abundance data collected during annual censuses. I calculated rates of calf production and young animal survival from ground composition counts and used these data to model the population and estimate

the role of emigration in population stabilization. I determined shifts in population distribution from radio telemetry surveys to document range expansion.

Chapter 2 presents a study of some seasonal strategies of muskoxen including shifts in distribution, changes in movements and activity levels, and habitat use. I used muskox locations from radio-relocation surveys to define seasonal shifts in population distribution. I used satellite telemetry to obtain frequent year-round locations of individual female muskoxen, rates of movement, and activity data. I delineated seasonal ranges of individual female muskoxen from the locations, calculated range overlap and distance, and determined habitat types within these ranges from a Landsat-TM vegetation map.

Chapter 3 presents results of a study to determine how and why mixed-sex groups of muskoxen disperse. I developed models to explain the process of dispersal in this expanding population by making predictions about attributes associated with individual dispersal events and shifts in population distribution. I used measures of animal abundance and changes in distribution to detect shifts in population distribution. I used data from annual composition counts to calculate rates of calf production and young animal survival. I used multi-year observations of marked females to determine individual dispersal events and reproductive histories over time. I calculated mean group size from observations made during radio-relocation surveys. I used these data to determine the validity of predictions made for each dispersal model.

CHAPTER 1.

DYNAMICS AND RANGE EXPANSION OF A REESTABLISHED MUSKOX POPULATION¹

ABSTRACT

Restoration of a large vertebrate to regions of former range was an opportunity to study processes of population expansion and colonization. Muskoxen (*Ovibos moschatus*) were returned to the Arctic National Wildlife Refuge (Arctic NWR) in northeastern Alaska in 1969-70 after an absence of over 100 years. In 1982-95, I documented changes in distribution and abundance of muskoxen and determined the relative importance of calf production, survival, and emigration on abundance in regions first occupied. I used annual censuses, counts of sex and age classes, and radiotelemetry surveys to determine exponential rates of increase and range expansion. From 1977 to 1981, muskoxen increased at an annual rate of 0.24 and calf production averaged 87 calves/100 adult females. From 1982 to 1986, mixed-sex groups still occupied the same regions, but rates of increase declined to 0.14 and calf production declined to 61 calves/100 adult females. After 1986, numbers of muskoxen in regions first occupied declined and may be stabilizing at <300 animals. Calf production continued to decline (49 calves/100 adult females in 1987-90 and 38 calves/100 adult females in 1991-96). Rates of calf and yearling survival did not decline, but were negatively correlated with snow depth in late spring. After 1986, dispersal of mixed-sex groups into other regions also contributed to the decline in muskox numbers in regions first occupied. In 1995, 647 muskoxen were seen in the study area from the

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Sagavanirktok River to the Clarence River. Throughout the total range of mixed-sex groups, about 800 muskoxen were observed in the 500 km between the Itkillik River west of Prudhoe Bay and the Babbage River in northwestern Canada. Muskox range expansion, population trends, and interactions with caribou should continue to be monitored.

INTRODUCTION

Muskoxen lived throughout Arctic Alaska during the Pleistocene and into the Holocene but disappeared from the Alaskan Arctic coast by the mid-1800's (Hone 1934). The elimination of the species from Alaska and the reduction of muskox numbers in Canada by the early 1900's raised concerns that the muskox may be extirpated throughout its range and resulted in efforts to restore and introduce populations in several Arctic areas (Klein 1988).

The species become reestablished in Alaska when muskoxen from Greenland were released on Nunivak Island near the western Alaskan coast in 1935-36 (Spencer and Lensink 1970). In March and April 1969, muskoxen were returned to regions of former range in northeastern Alaska when 51 animals from Nunivak Island were released during 4 different events at Barter Island, near the coastal plain of the Arctic NWR. In June 1970, 13 more muskoxen were released at Kavik River, about 25 km west of the refuge (Jingfors and Klein 1982).

Studies of indigenous muskox populations in Canada, (Case et al. 1989, Gunn et al. 1991) and Greenland (Boertmann et al. 1992) and introduced or re-established populations in western Greenland (Olesen 1993), Quebec (Le Hénaff and Crête 1989), Russia (Yakushkin 1989) and Alaska (Smith 1989a) showed that world-wide numbers of muskoxen increased dramatically since the early 1900's. Overexploitation by humans and severe weather were likely causes of population declines. Hence, the return of muskoxen to Alaska provides an opportunity to study factors associated with

population expansion. I evaluated the role of reproduction, survival, and emigration in determining rates of increase in an expanding, reestablished population of muskoxen in northeastern Alaska to determine what factors were responsible for changes in abundance in regions first occupied.

STUDY AREA

The study area, between the Sagavanirktok River (148° 35' W) in eastern Arctic Alaska and the Clarence River (141° 00' W) near the United States-Canada border was bounded on the north by the Beaufort Sea (70° 05' N), and on the south by the mountains of the Brooks Range (69° 25' N) (Fig. 1). This area of 24,700 km² was east of the oil fields at Prudhoe Bay and included the coastal plain of the Arctic NWR. The land was underlain by continuous permafrost and was snow covered for 8-9 months each year. Vegetation was Arctic tundra. Willows (*Salix sp.*), forbs, and graminoids grew on partially vegetated gravel bars of rivers. Tussock-shrub, low shrub, and shrub-heath communities occurred on the slopes of rolling hills, and sedge-moss communities dominated poorly drained flat areas (Bliss 1981). Major features of terrain included braided north-flowing rivers and flood plains, foothills, hilly coastal plains, thaw-lake plains, and mountains (Walker et al. 1983).

METHODS

Animal Distribution

I determined range expansion of muskoxen from changes in distribution of mixed-sex groups (the reproductive segment of the population). Mixed-sex groups are composed of adult females, subadult animals, and often 1 or more adult males (Reynolds 1993). I did not include adult males that permanently dispersed beyond the distribution of mixed-sex groups.

I radiocollared adult muskoxen to determine their distribution. I captured animals with Carfentanyl citrate and xylazine (CERVIZINE™, Wildlife Pharmaceuticals, Fort Collins, Colorado USA) administered from projectile syringes fired from helicopters. Study methods were approved by the University of Alaska Fairbanks (UAF) Animal Care and Use Committee. Each year from 1982 to 1994, I then relocated 18 to 24 radiocollared muskoxen 6 times/ year in February, March, May, June, August, and October or November. During these survey flights, which followed predetermined routes along major drainages, I recorded locations of mixed-sex groups of muskoxen (marked, unmarked) via a Global Positioning System (GPS) mounted in the aircraft, or on 1:63,360 scale maps. Locations were recorded to the nearest 0.5 km. I compared the distribution of muskoxen in 1982-93 with distribution in 1969-81 (Roseneau and Warbelow 1974; Arctic NWR unpubl. data).

I used the adaptive-kernel technique (Worton 1989) calculated via program CALHOME (Kie et al. 1996) to delineate the size and location of regions used by mixed-sex groups of muskoxen in 1969-81, 1982-85, 1986-89 and 1990-93. Locations were not significantly autocorrelated ($P > 0.10$), based on the results of multi response sequence procedure tests (program BLOSSOM; Slauson et al. 1991). I defined core areas of use (Wray et al. 1992) as the 70% adaptive-kernel contour and total range as the 95% contour.

I defined regions first occupied as regions 50 km wide that were colonized by mixed-sex groups of muskoxen soon after their release and were inhabited in 1969-81 (Fig 1). I defined regions occupied later as regions that were not used in 1969-81, but were subsequently colonized by mixed-sex groups (Fig. 1).

Population Abundance and Composition

I conducted annual precalving censuses in 1982-95 to determine animal abundance in regions first occupied and regions occupied later. I systematically

searched all major river drainages and adjacent uplands between the Canning River and the Canadian border via a Cessna 185TM airplane flying 300 m above ground level (AGL) in late March or early April in all years. Difficult logistics and high costs associated with working in the Arctic environment precluded replicate censuses within a year. In 1986, I expanded the census area westward to the Sagavanirktok River because radiocollared muskoxen dispersed into these regions. I compared estimates of abundance in 1982-95 with estimates in 1972-81 (Roseneau and Warbelow 1974, Jingfors and Klein 1982, D. E. Ross, Arctic NWR, Fairbanks, Alaska, unpubl. rep.). I calculated average exponential rates of increase by plotting the natural logarithms of population size over time, using linear regression to determine the slope, or from the difference between natural logarithms of population estimates made at 2 different times, divided by the number of years between the 2 estimates (Caughley and Sinclair 1994).

In late June, 1983-95, I calculated calf production and calf and yearling survival from composition data collected in regions first occupied. I classified animals from the ground into 4 categories of age (< 1 yr, 1 yr, 2 yr, > 2 yr [adult]) and recorded sex for all animals older than yearlings. I compared these data with muskox composition collected from 1972 to 1981 (Roseneau and Warbelow 1974; Jingfors and Klein 1982). I used calves per 100 females > 2 years old (ad F) as a measure of calf production and an estimate of calves present in the population. I calculated survival rates of calves and yearlings by dividing estimated numbers of calves or yearlings by estimated numbers of yearlings or 2-year-olds in successive years. I estimated numbers in these age classes from yearlings per 100 females > 3 years old and 2-year-olds per 100 females > 4 years old. Numbers of females > 3 years old at time $t+1$ and > 4 years old at time $t+2$ were the number of females > 2 years old at time t minus known and estimated mortalities.

Modeling

I developed interactive models to reconstruct the muskox population by using different schedules of calf production and survival. I assumed the population began in 1970 with 37 animals (maximum. no. seen after release) and that sex ratios were equal at birth. To estimate an intrinsic (maximum) rate of increase for the muskox population, I assumed all females > 2 years old produced one calf annually in 1970-95, that yearlings and two-year-olds did not reproduce (Reynolds unpubl. data), and that males died at age 12 and females died at age 18 (Olesen 1993, this study). A second maximum growth model assumed 50% of 2-year-old females also produced 1 calf each year (Jingfors and Klein 1982, Olesen 1993).

To estimate the effect of calf production and survival on rates of increase, I reconstructed the muskox population using calf:female ratios and survival rates of calves and yearlings calculated from composition data collected in regions first occupied. For this model, I assumed that all animals > 3 years old survived until males died at age 12 and females died at age 18 and that all 3-year-old females and 70% of 3-year-old males remained in the study area (Smith 1989b, Reynolds, unpubl. data). To determine the effect of emigration losses, I compared muskox abundance predicted by the reconstructed population model to numbers of muskoxen observed during spring censuses in regions first occupied. Changes in the observed rate of increase reflected losses from emigration as well as changes in reproduction and survival.

Statistical Tests

I used linear regression and correlation (PROC REG; SAS Institute 1988) to compare measures of productivity, to determine trends in productivity and survival over time, to measure and compare observed rates of increase with those predicted by reconstructed population models, and to examine the relation between snow measurements, productivity, and survival. I used *t*-tests (PROC TTEST; SAS Institute

1988) to examine differences in snow measurements in years of high and low productivity and survival. I compared the slopes of regression lines calculated for observed and predicted abundance in regions first occupied by dividing the difference between the slopes by the standard error of the difference between the regression coefficients (Zar 1984: 292).

RESULTS

Animal Abundance and Rates of Population Growth

Muskoxen released at Barter Island in 1969 were primarily young: 39% yearlings (10 M;15 F), 14% 2 years old (4 M;5 F), 39% 3 years old (11 M;14 F) and 8% adults (all M). No more than 34 (67%) of these 51 muskoxen remained alive in the study area after a few months. Ten mortalities occurred soon after the release events and at least 7 animals (probably males) left the study area. After the release of 13 additional muskoxen at Kavik River in June 1970, the initial population in northeastern Alaska was a maximum of 47 individuals. Up to 37 animals were seen from 1969 to 1974 (Roseneau and Warbelow 1974, D. E. Ross, Arctic NWR, unpublished data). In regions first occupied, numbers of muskoxen expanded slowly during the first few years after the their release, then grew rapidly for almost a decade (Fig. 2). The greatest rate of increase occurred between 1977 and 1981 when the population increased at a rate of 0.24 (Table 1). The reconstructed population model of maximum growth (r_m) had a rate of increase of 0.27 ($r^2_{24} = 0.99$), without 2-year-olds reproducing, or 0.29 ($r^2_{24} = 0.99$), if 50% of 2-year-old females were assumed to reproduced, suggesting the population approached but did not reach r_m during the period of fastest growth.

From 1982 to 1986, in regions first occupied, the annual rate of increase was 0.14, and a maximum of 386 muskoxen was counted in 1986. After 1986, the rate of increase was negative because numbers of muskoxen declined (Table 1, Fig. 2).

Numbers of muskoxen in regions first occupied may be stabilizing at <300 or declining slowly (Fig. 2). From 1986 to 1990, in regions occupied later, numbers of muskoxen increased at rates almost double the rates predicted by the maximum growth model and continued to increase from 1990 to 1995 (Table 1, Fig 2.).

In 1995, I counted 228 muskoxen in regions first occupied and 419 in regions occupied later in the study area (Fig. 2). In addition, about 150 other muskoxen were observed outside the study area in 1995 in northwestern Canada (Department of Renewable Resources Yukon Territorial Government 1996) and in north-central Alaska west of the Sagavanirktok River (C.G. Johnson et al. 1997. Wildlife studies on the Colville River delta, 1996, unpubl. Report. Arco Alaska, Fairbanks, Alaska, USA). These numbers indicate that about 800 muskoxen were present in the total range occupied by mixed-sex groups in 1995. Assuming an initial population of 37 in 1973, numbers of muskoxen throughout the total range of mixed-sex groups in northeastern Alaska and northwestern Canada increased at rate of 0.14 from 1973 to 1995 ($r_{21}^2 = 0.93$).

Calf Production and Survival

Calf production was the only source of increase in muskox numbers in regions first occupied. Ratios of calves per 100 adult females were highest from 1977 to 1980, 6-10 years after the muskox releases in 1969 and 1970 (Table 2), but declined over time ($r^2 = 0.75$, $P = 0.0001$, $n = 17$).

From 1983 to 1995, mean survival in regions first occupied ranged from 0.75 to 0.85 for calves and 0.69 to 0.72 for yearlings (Table 2). Calf production and survival of calves and yearlings varied annually and followed similar trends (calf productivity vs. calf survival: $r_s = 0.55$, $P = 0.06$, $n = 12$; calf productivity vs. yearling survival: $r_s = 0.58$, $P = 0.06$, $n = 11$; calf survival vs. yearling survival: $r_s = 0.82$, $P = 0.002$, $n = 11$) (Fig. 3). The largest number of deaths of radiocollared females occurred in 1989 (5 of 23) and 1995 (6 of 25), years in which calf production and

young animal survival were also low (Fig 3). Calf productivity in regions first occupied continued to decline from 1983 to 1995 ($r^2 = 0.46$, $P = 0.01$, $n = 13$), but calf and yearling survival did not decline during the same period (calf survival: $r^2 = 0.01$, $P = 0.71$, $n = 13$; yearling survival: $r^2 = 0.01$, $P = 0.82$, $n = 13$) (Fig.3).

Over time, the interval between successful reproduction by radiomarked female muskoxen increased. In 1982-86, 46% (6 of 13) radiocollared females reproduced annually for 3-4 years, but during the next decade, this percentage decreased to 26% (7 of 27) in 1987-95. The percentage of radiocollared females failing to reproduce in 3 or more consecutive years increased from 0% (0 of 13) in 1982-86 to 22% (6 of 27) in 1987-95.

Female muskoxen in northeastern Alaska were long-lived. Three females released on Barter Island in 1969 were recaptured in 1982, and monitored until they died at age 17-19 years of age, in 1984 and 1985. Adult female mortalities likely increased after 1985 as animals reached their maximum life-span.

Population Reconstruction

From 1972 to 1986, numbers of muskoxen predicted from the reconstructed population model fit a linear model ($r^2_{14} = 0.99$, $P < 0.0001$) as did numbers observed during population censuses ($r^2_{12} = 0.99$, $P < 0.0001$). Rates of increase, calculated from the slopes of the regression lines, were both 0.20, and the slopes of the two lines were not different ($t_{11} = 0.04$, $P > 0.50$). From 1987 to 1995, numbers of muskoxen predicted by the reconstructed population model continued to increase, but at a slower rate (0.06) ($r^2_5 = 0.95$, $P < 0.0001$). This decline reflected the effect of declining calf production and annual variability in survival because these variables were incorporated into the model. Observed abundance in regions first occupied, however, was even lower than predicted. Numbers of muskoxen declined and stabilized from 1987 to 1995, no longer fitting a linear model ($r^2_5 = 0.24$, $P = 0.1753$), indicating that actual rate increase in regions first occupied was zero or

negative. The difference between numbers of muskoxen predicted by the reconstructed population model and numbers actually observed were likely additional losses from emigration. Most (70%) of the decline in the rate of population increase from 1986 to 1995 could be explained by observed declines in calf production and annual variability in survival. Emigration accounted for about 30% of the change in the rate of increase.

Emigration and Range Expansion

Beginning in 1985, small numbers of muskoxen in mixed-sex groups were observed in regions outside those first occupied, but a large pulse of dispersal occurred in 1986-87 and additional emigration of mixed-sex groups likely took place in 1988-89, 1991-92, and 1994-95. Rates of increase from 1986 to 1990 in regions occupied later (Table 1) were almost twice that predicted by maximum growth models, which indicated that the increase in numbers of animals was the result of immigration. Movements of radiomarked female muskoxen confirmed that mixed-sex groups moved from regions first occupied into regions occupied later (P. E. Reynolds unpubl. data).

The emigration of mixed-sex groups out of regions first occupied resulted in shifts in population distribution and range expansion. Muskoxen released at Barter Island and Kavik River in 1969 and 1970 soon coalesced into 3 mixed-sex groups that occupied 3 different regions along the Tamayariak--Canning Rivers, the Sadlerochit River, and the Okerokovik--Angun drainages of the Arctic NWR coastal plain from 1969 to 1981 (Fig. 4). For the next 4 years, mixed-sex groups remained in these regions (Fig. 4), although numbers of animals increased from <43 in 1972 to >300 in 1985. After 1985, mixed-sex groups began to expand westward and eastward into other regions of the study area (Fig. 4C) and beyond the study area into northwestern Canada and north-central Alaska. By 1990-93, the total range within the study area used by mixed-sex groups extended from the Sagavanirktok River to the Canadian border (Fig. 4D). Total range occupied by mixed sex groups within the study area

tripled in size between 1982-85 and 1990-93 and the size of core areas expanded by a factor of 5 (Table 3). Over time, the distribution of mixed-sex groups and total numbers of muskoxen expanded more rapidly in the western portion of the study area. By 1995, the total distribution of mixed sex groups of muskoxen extended 500 km from the Itkillik River, west of the study area, to beyond the Babbage River in northwestern Canada (Fig. 5).

DISCUSSION

Muskoxen have been successfully returned to regions of former range in northeastern Alaska, and reproducing animals have expanded their range into north-central Alaska and northwestern Canada. In this study, the average exponential rate of increase of 0.14 over 22 years throughout the total range of mixed-sex groups was similar to long-term rates calculated for other expanding populations of muskoxen. On Nunivak Island, muskoxen increased at a rate 0.16 in 1935-68 (Spencer and Lensink 1970), and on Banks Island, in northwestern Canada, the muskox population grew at a rate of 0.13 in 1972-89 (Gunn et al. 1991).

Growth of the population of muskoxen in this study occurred in 3 stages: (1) slow growth for a few years immediately following the release; (2) an irruptive phase of rapid growth for about a decade; and (3) decline and stabilization in regions first occupied concurrent with emigration of mixed sex groups and expansion into additional regions during the second decade.

Factors which likely influenced the initial slow growth of the population from 1970 to 1975 were capture-related stress, adjustments to new landscapes, and the dispersal of mature males. Severe weather conditions also may have affected calf production and survival of all age classes during these years. Muskoxen on Nunivak Island in Alaska and on Wrangel Island in Russia also increased slowly during the first years after their release (Spencer and Lensink 1970, Klein 1988).

During the irruptive phase of this study, the rate of increase approached rates predicted by the maximum growth models in some years. Jingfors and Klein (1982) attributed early sexual maturity and high rates of reproduction and survival observed during the rapid growth phase to highly nutritious forage in unexploited habitats. Populations reach intrinsic rates of growth only when competition for food is negligible (Caughley and Sinclair 1994). In 1979, at the peak of the growth phase, Jingfors and Klein (1982) reported 100% reproduction in all adult females on the Sadlerochit River and observed 2 of 4 2-year-old females with calves. In a population of introduced muskoxen in West Greenland, Olesen (1993) estimated 50% of 2-year-old females produced calves in a region with abundant high-quality forage and low amounts of snow.

High percentages of young females in the released population and high rates of survival also contributed to the rapid growth phase observed in this study. Only 4 of 7 muskox calves produced in 1972 survived as yearlings (Roseneau and Warbelow 1974), but Jingfors and Klein (1982) reported 100% overwinter survival of calves and 83% survival of yearlings on the Sadlerochit River in 1979-80. Olesen (1993) also found little winter mortality in calves and yearlings in a rapidly growing West Greenland population of muskoxen.

The decline and stabilization of muskox numbers in regions first occupied occurred because of declining calf production, changes in survival rates, and the dispersal of mixed-sex groups into additional regions. Declining forage conditions from intraspecific competition could have affected calf production if adult females were unable to regain enough body mass to come into estrous (White et al. 1997), or had insufficient body fat to maintain a pregnancy or provide sufficient milk to rear young. Muskox calves were born in April and May when weather conditions were still severe and only low-quality winter forage was available for several weeks after parturition. Because calf productivity was measured in late June after mortality of new born calves

had already occurred, it was not possible to determine if changes in calf:female ratios were due to declining fecundity or increased mortality of young calves.

In this study, weather likely affected calf production and animal survival. Calf and yearling survival were negatively correlated with snow depths and snow disappearance dates measured in May and June at a foothills site 90 km west of the study area (Kane 1997) (Calf survival and snow depth: $r_s = -0.61$, $P = 0.04$; calf survival and snow disappearance: $r_s = -0.62$, $P = 0.04$; yearling survival and snow depth: $r_s = -0.90$, $P = 0.0002$; yearling survival and snow disappearance: $r_s = -0.84$, $P = 0.0012$). Mean snow depths were greater ($t_s = -4.29$, $P = 0.0085$) in years of low calf production and survival (1986, 1989, 1992 and 1995) compared with years of relatively high production and high survival (1985, 1988, 1990 and 1993). Deep snow limits the availability of winter forage (Wilson 1992) and adds to energetic costs of foraging and movement. Weather events in the Canadian Arctic and on Nunivak Island resulted in large numbers of mortalities and breeding pauses in muskoxen (Spencer and Lensink 1970, Gray 1987). Deep snow, winter thaws, and icing conditions reduced forage availability and resulted in high mortality and low productivity of muskoxen on islands in the Canadian Arctic (Parker et al. 1975).

Increased predation could have contributed to the decline in numbers of muskoxen in regions first occupied. For several years after release, predation levels likely were low. Brown bears (*Ursus arctos*) and gray wolves (*Canis lupus*) probably were unaccustomed to killing muskoxen, which had been unavailable in northeastern Alaska for >100 years. Also muskox densities were low for several years after their release. After 1986, several incidents of predation or scavenging by brown bears on all sex and age classes of muskoxen were documented (P. E. Reynolds unpubl. data). Young calves were killed directly by brown bears and also likely died when they were left behind by muskoxen fleeing from a brown bear attacking an adult female. Male bears emerge from dens during the muskox calving period, and young calves may be

vulnerable to predation (Clarkson and Liepins 1993). Predation by wolves was also documented after 1986 during this study. Human harvest of muskoxen in the study area from 1986 to 1997 was about 3% of the population. Regulations limited the harvest to males, but some females were also killed.

Growth of the muskox population in this study began to slow within a decade, and animal abundance declined in regions first occupied within 17 years after release. By contrast, a population of muskoxen introduced to West Greenland was still irrupting 25 years after animals were released. This irruption was fueled by high rates of calf production, including 50% reproduction by 2-year-old females, annual reproduction by females >2 years, and very low mortality of calves and yearlings (Olesen 1993). The West Greenland study area also had abundant high quality forage, no predators, and very low snowfall throughout the winter (Olesen 1993). In northeastern Greenland where deeper snow, longer snow seasons, and predators were present, most females produced calves in alternate years (Thing et al. 1987). Muskoxen in this study had access to high-quality forage (Robus 1981), but foraged through snow for 9-10 months of the year and were subjected to annual variability in weather conditions and predation from brown bears and wolves. Overall, declining calf production and annual variability in survival likely had the greatest effect on slowing the rate of increase of this expanding muskox population. But emigration also played an important role in the stabilization of muskox abundance in regions first occupied.

MANAGEMENT IMPLICATIONS

Regions first occupied by muskoxen in this study coincided with that portion the coastal plain of the Arctic NWR being considered exploratory drilling for oil and gas and possible development of petroleum resources. Because muskoxen are one of the few large vertebrates present in these regions year-round, they are vulnerable to potential effects from petroleum development and other human activities. The

stabilization of muskox numbers at < 300 and the declining trend in calf production indicate that this population should continue to be monitored. Human activities should avoid areas occupied by muskoxen, particularly before, during and after the calving season (Apr to mid-Jun).

Although muskoxen have become successfully reestablished in northern Alaska, range expansion is a slow process. Twenty-eight years after the first releases, < 1000 muskoxen occupy $< 20\%$ of their former range on the North Slope of Alaska. This same area is used seasonally by $> 720,000$ caribou, whose numbers almost quadrupled during the decades since muskoxen were reestablished. As muskoxen in northern Alaska expand into new regions, local residents have expressed concern that numbers of muskoxen will increase to levels like those on Banks Island, Canada ($> 65,000$ in 1995, A. Gunn, et al. 1995. Muskox and caribou numbers and distribution from 1992 to 1995 in Canada's Northwest Territories, unpubl. report. Department of Renewable Resources, Government of the Northwest Territories, Yellowknife, Northwest Territories) and that competition or negative interactions will result in the exclusion of migratory caribou from seasonally shared ranges. The decline or stabilization of muskox numbers in regions first occupied in northeastern Alaska within 17 years after the release, as well as the low rates of increase in northwestern Alaska indicate that population levels of this magnitude are unlikely to occur in northern Alaska. Nonetheless, muskox range expansion and rates of population growth should continue to be monitored and investigations of caribou and muskox distributions and interactions should continue.

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Table 1. Exponential rates of increase (r)^a for a reestablished population of muskoxen in regions first occupied and regions occupied later in northeastern Alaska, 1972-95.

Years	Regions first occupied			Regions occupied later		
	Number of muskoxen			Number of muskoxen		
	Start	End	r	Start	End	r
1972-73 ^b	28	29	0.03	1 ^c	2 ^c	
1977-81 ^d	71	183	0.24	1 ^c	3 ^c	
1982-86	219	386	0.14	nd	22 ^c	
1986-90	386	273	-0.09	22 ^c	198	0.55
1990-95	273	228	-0.04	198	419	0.15

^a $r = (\log_e N_t - \log_e N_0)/t$ (Caughley and Sinclair 1994)

^b data from Roseneau and Warbelow (1972)

^call males

^ddata from Jingfors and Klein (1982)

^e10 were in bull groups

Table 2. Mean calf production and calf and yearling survival for muskoxen in regions first occupied in northeastern Alaska, 1972-95.

Period	<i>n</i> ^a	Calves:100			
		Calves:100 F > 2 yr old	muskoxen older than calf	Calf survival	Yearling survival
1972-73 ^b	37		22		
1977-80 ^c	118	87	29		
1983-86	321	61	25	0.85	0.69
1987-90	254	49	22	0.75	0.72
1991-95	225	38	17	0.82	0.71

^aMean number of muskoxen classified during period.

^bData from Roseneau and Warbelow (1974).

^cConservative estimates based on number of yearlings seen the following spring (D. E. Ross, Arctic NWR, unpubl. data).

Table 3. Changes in the size of the total range (95% adaptive-kernel contour) and centers of population distribution (70% adaptive-kernel contour) occupied by mixed-sex groups of muskoxen in the study area, northeastern Alaska, 1969-93.

Years	<i>n</i> ^a	Area size (km ²)	
		Total range ^b	Centers of distribution ^c
1969-81	180	11,670	2,571
1982-85	295	7,712	2,405
1986-89	346	24,950	6,594
1990-93	406	23,650	11,340

^aNumber of observations used to calculate area.

^bLocations within 95% adaptive-kernel contour.

^cLocations within 70% adaptive-kernel contour.

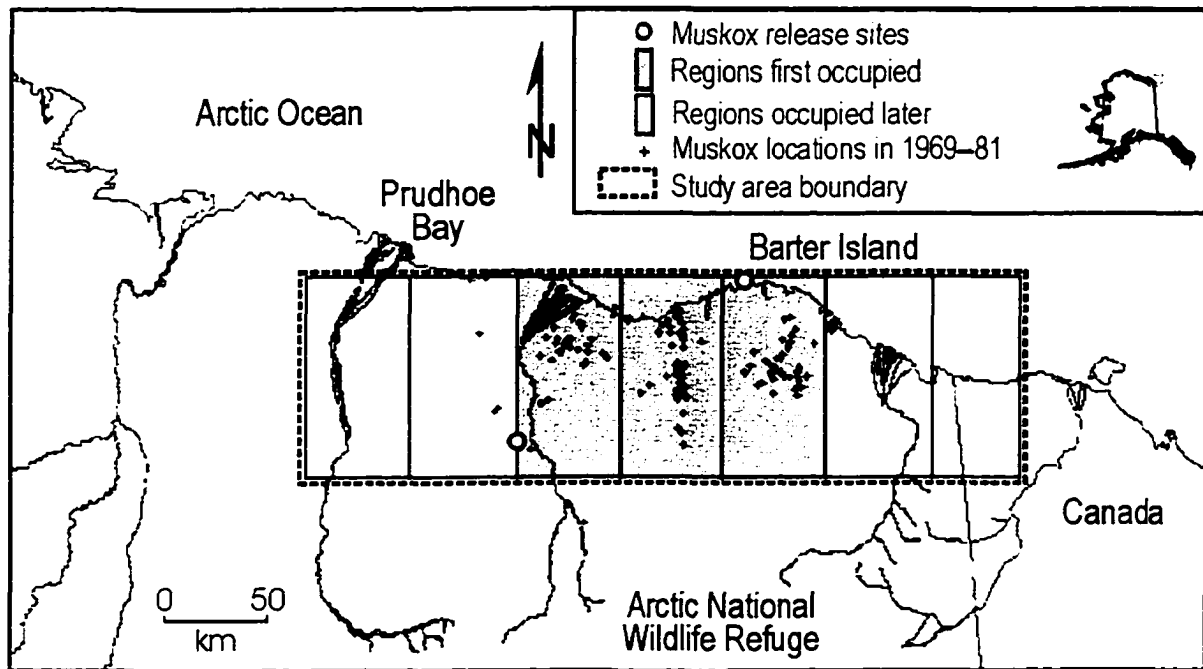


Fig. 1. Muskox study area in northeastern Alaska. Regions first occupied were regions that encompassed locations of mixed-sex groups in 1969-81. Regions occupied later were not inhabited by mixed-sex groups in 1969-81.

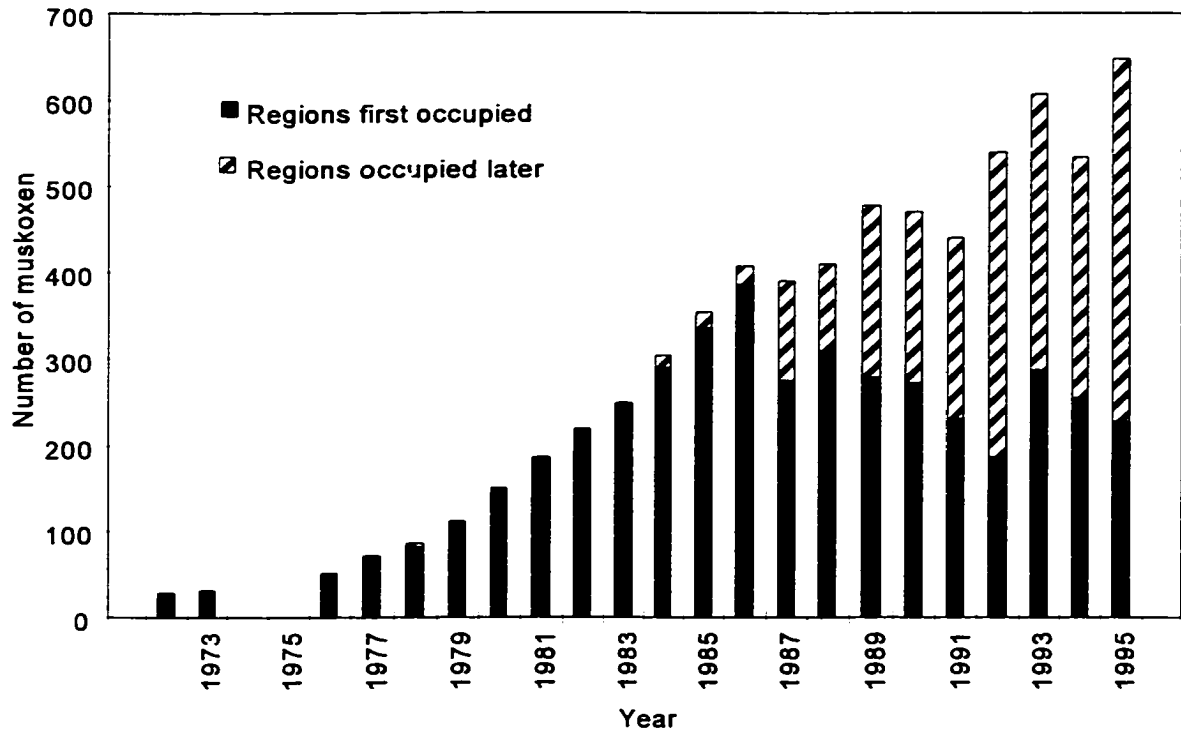


Fig. 2. Number of muskoxen in regions first occupied and regions occupied later in northeastern Alaska, 1972-95.

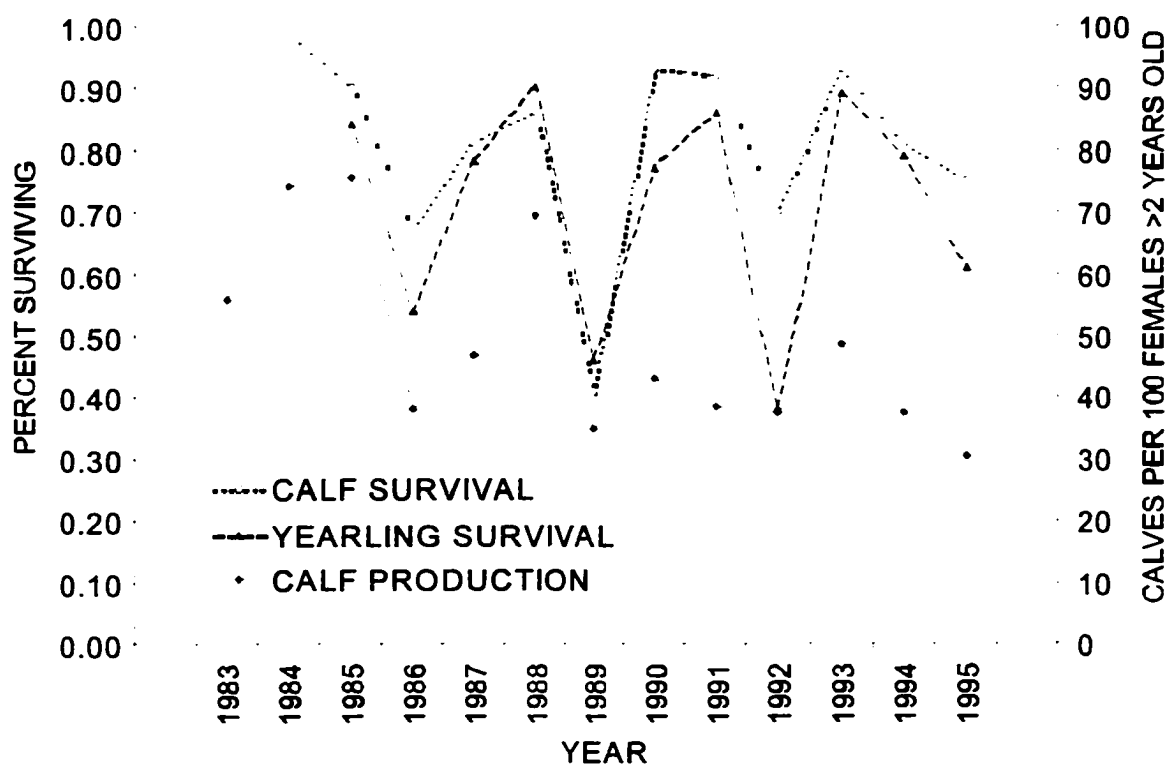


Fig. 3. Annual variability in muskox calf production and survival of calves and yearlings in regions first occupied in northeastern Alaska.

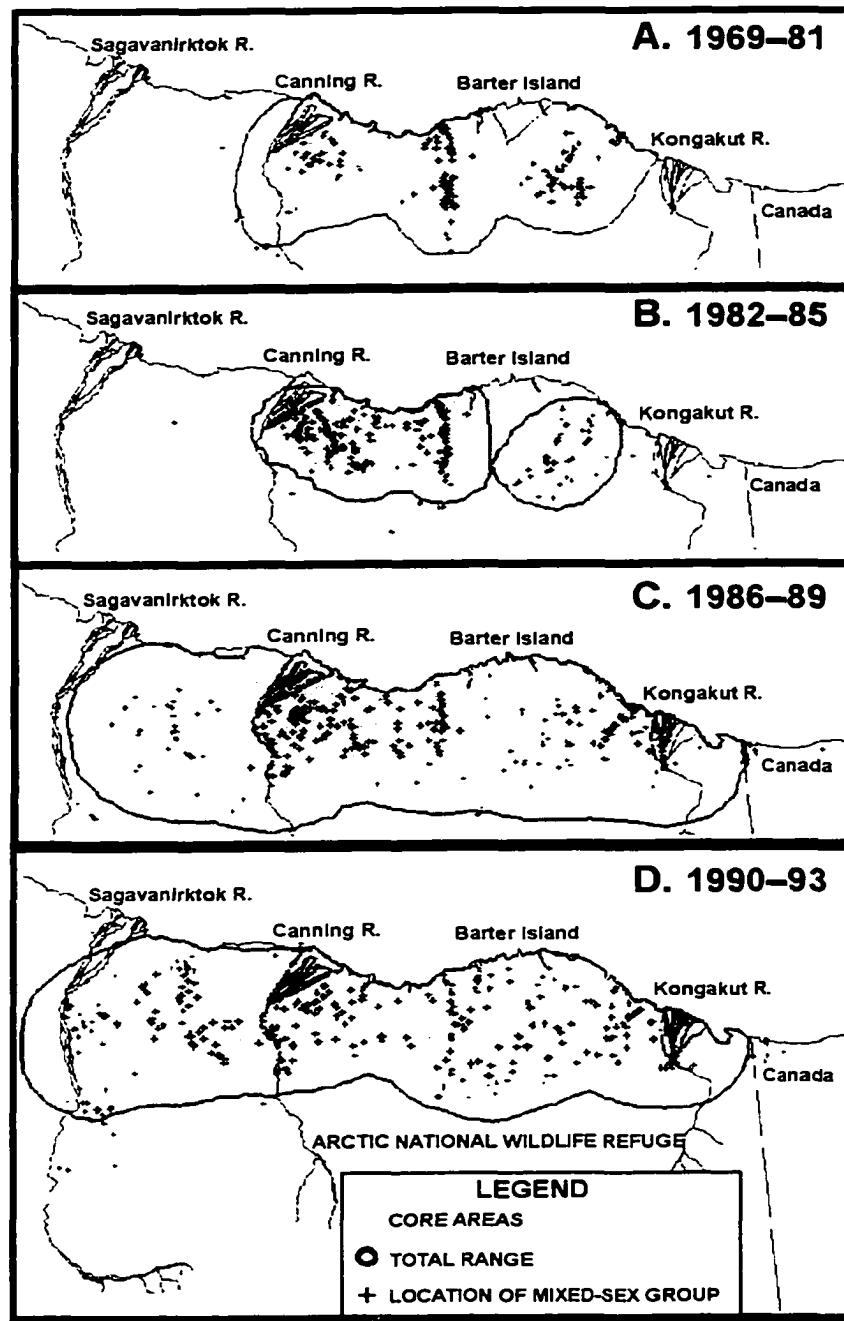


Fig. 4. Range expansion of mixed-sex groups of muskoxen in the study area in northeastern Alaska.

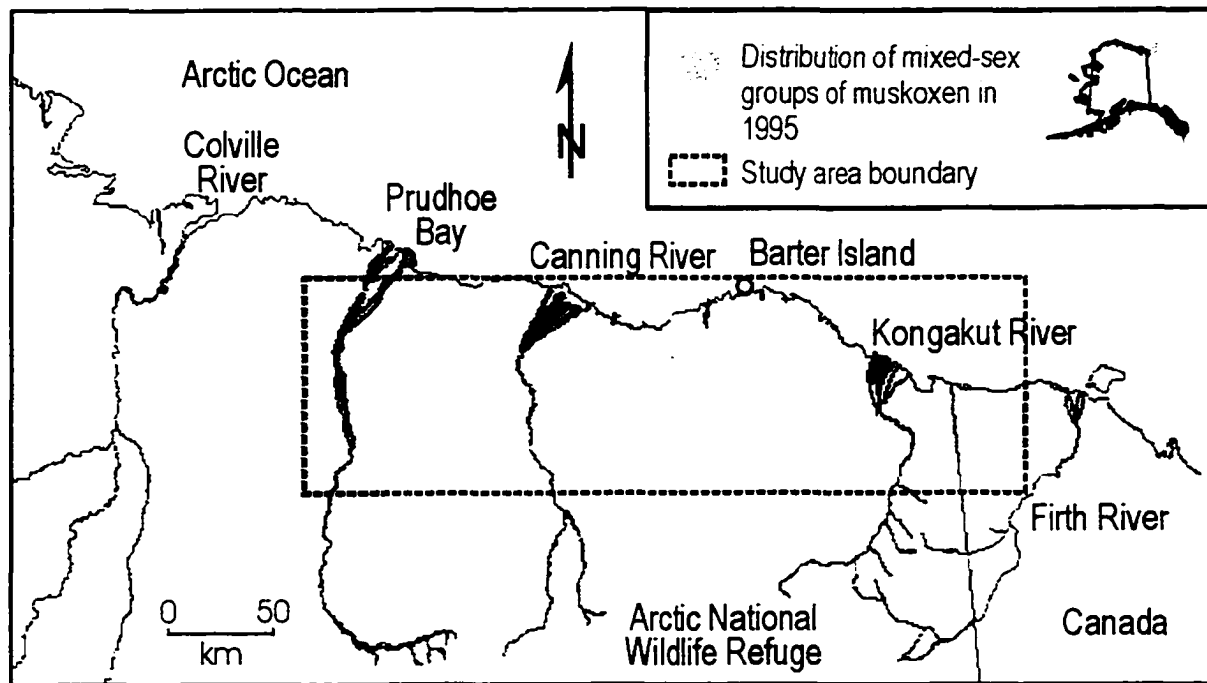


Fig. 5. Total range of mixed-sex groups of muskoxen in northeastern Alaska and northwestern Canada in 1995.

CHAPTER 2.

SEASONAL DISTRIBUTION, ACTIVITY, AND HABITAT USE OF MUSKOXEN IN NORTHEASTERN ALASKA

ABSTRACT

Seasonal strategies include means by which animals adapt to living in extreme environments. I studied seasonal differences in distribution, movements, activity patterns, and habitat use in a population of muskoxen (*Ovibos moschatus*) in northeastern Alaska using location and activity data from satellite-collared females, population distributions from radio-relocation surveys, and land cover and terrain types derived from Landsat-TM maps. In summer (late June to mid-September) female muskoxen occupied larger core areas ($\bar{x} = 223 \text{ km}^2$), and had higher rates of movement ($\bar{x} = 2.6 \text{ km/day}$) and activity ($\bar{x} = 19 \text{ counts/min}$). Movement rates and activity indices reached a peak in July, just prior to the mating season in August and early September. In winter (late September to mid-March) and calving (late March to early June), muskoxen remained in small core areas (mid-winter $\bar{x} = 31 \text{ km}^2$, calving $\bar{x} = 28 \text{ km}^2$), moved less (mid-winter $\bar{x} = 1.4 \text{ km/day}$, calving $\bar{x} = 1.1 \text{ km/day}$) and reduced activity (mid-winter $\bar{x} = 12 \text{ counts/min.}$, calving $\bar{x} = 11 \text{ counts/min}$). All seasonal distribution of the muskox population overlapped. Muskoxen selected (use > availability) riparian and moist sedge vegetation along rivers in all seasons, and avoided upland shrub in foothills, except in the calving season. These seasonal strategies, as well as adaptations to cold and the ability to subsist on low-quality forage, allow muskoxen to survive the environmental extremes of the Arctic.

INTRODUCTION

Arctic animals must cope with the constraints of a rigorous environment. I examined some seasonal strategies of a large mammal living year-round at the northern edge of the distribution of terrestrial vertebrates. Seasonal shifts in distribution, habitat use, and activity are considered behavioral adaptations by which animals attempt to optimize food intake and avoid conditions that may reduce survival. Many species of ungulates migrate between summer and winter ranges (Fancy et al. 1989, Andersen 1992, Nicholson et al. 1997). This strategy allows animals to take advantage of the seasonal availability of high quality forage and to avoid adverse conditions including predation (Sinclair 1992, Dingle 1996). In northeastern Alaska, on the coastal plain of the Arctic National Wildlife Refuge (Arctic NWR), most birds and large mammals, including caribou (*Rangifer tarandus*), are present only during the short snow-free summer, and migrate long distances or hibernate to avoid the rigors of the arctic winter. In contrast, muskoxen are resident in this area where winter conditions exist for > 8 months.

Muskoxen were extirpated from Alaska by the late 1800's, but were re-established in northeastern Alaska by translocation of animals from Nunivak Island in 1969 and 1970 (Klein 1988). The reintroduction occurred on the coastal plain of the Arctic NWR that may contain significant petroleum resources. Understanding seasonal patterns of muskox use of the landscape in the Arctic NWR is needed to evaluate and minimize possible impacts on this resident population if these resources are developed.

In northeastern Alaska, the growing season is only 6-8 weeks long, from mid-June to late July or early August. During this time, muskoxen feed on high quality green forage that grows rapidly under 24 hours of daylight. For 8-9 months of the year, access to forage is restricted by snow. I predicted that muskoxen in the Arctic NWR used different areas and habitats in summer and winter.

Energy conservation is imperative in species living under the extreme conditions of the Arctic. Muskoxen are an energetically conservative species (Klein 1992), and seasonal reductions in movements and activity are mechanisms for conserving energy. Because muskoxen remain on the coastal plain of the Arctic NWR throughout the winter, I predicted that muskoxen would move less and would be less active in winter than in summer, and occupied smaller areas in winter than in summer. I tested these predictions by examining seasonal differences in population distribution, seasonal habitats associated with individual home ranges, and seasonal differences in the movements and activity patterns of individuals.

STUDY AREA

The study area, between the Canning River ($146^{\circ} 30' \text{ W}$) and the Canadian border ($141^{\circ} 0.0' \text{ W}$) in northeastern Alaska, was bounded on the north by the Beaufort Sea ($70^{\circ} 05' \text{ N}$) and on the south by the mountains of the Brooks Range ($69^{\circ} 25' \text{ N}$). This area of $14,700 \text{ km}^2$ was east of the oil fields at Prudhoe Bay and included the coastal plain of the Arctic NWR. The land was underlain by continuous permafrost and was snow-covered for 8-9 months each year. Vegetation was Arctic tundra. Willows (*Salix sp.*), forbs, and graminoids grew on partially vegetated gravel bars of rivers. Tussock-shrub, low shrub and shrub-heath communities occurred on the slopes of adjacent rolling hills, and sedge-moss communities dominated flat poorly drained areas (Bliss 1981). Major features of this terrain included braided north-flowing rivers and flood plains, foothills, hilly coastal plains, thaw-lake plains, and mountains (Walker 1983).

METHODS

Seasonal Distribution

Seasons as defined in this study were periods of different ecological and biological conditions (Table 4). The calving season (late March to mid-June) included pre-calving, calving and post-calving periods. In the summer season (late June to mid-September), the plant growing period occurred and mating took place. In the early winter season (late September to mid-November), day length decreased and snow and cold weather were present. In the mid-winter season, (late November to mid-January), the sun was below the horizon for 24 h/d. In the late winter season (late January to mid-March), temperatures reached yearly minimums ($< -25^{\circ}\text{C}$), but day length increased (Table 4).

I used marked animals to determine the seasonal locations of muskoxen and captured muskoxen using immobilizing drugs (Carfentanyl citrate and xylazine; CERVIZINE™, Wildlife Pharmaceuticals, Fort Collins, Colorado) delivered by projectile syringes from helicopters. Study methods were approved by the University of Alaska Fairbanks Animal Care and Use Committee.

To identify population distribution in different seasons, I maintained 19-25 radiocollared muskoxen in the population each year from 1982 to 1995 and flew 4 to 6 radio-relocation surveys each year in calving, summer, early winter and late winter seasons. Animals were not located in mid-winter because of darkness, severe weather conditions, and the remoteness of the study area. Locations of muskoxen, both marked and unmarked, observed during these surveys were determined via a Global Positioning System (GPS) mounted in the aircraft, or plotted on 1:63360 scale maps to within the nearest 0.5 km.

The definition of seasonal home ranges and seasonal movement rates required frequent year-round locations of individual animals. I fitted 15 different adult female muskoxen with ultra high frequency platform transmitter terminals located by satellite

(Fancy et. al 1988, Reynolds 1989), and monitored 3 to 5 of these satellite collared muskoxen each year from October 1986 to March 1992,. Satellite collars transmitted information every second or third day for 6 hr/day (0900-1500 hr Alaska Standard Time).

I used an adaptive-kernel technique (Worton 1989) calculated via program CALHOME; Kie et al. 1996) to identify seasonal distribution of the population based on data from radio relocation surveys and to delineate seasonal home ranges of individuals carrying satellite collars. Locations were not significantly autocorrelated ($P > 0.05$), based on Multi response Sequence Procedure tests (program BLOSSOM; Slauson et al. 1991). I used the 95% adaptive-kernel contour to delineate boundaries of individual home ranges, and the 70% adaptive-kernel contour to find seasonal population distributions and to define core areas of use within individual home ranges (Wray et al. 1992). Although home ranges of individuals were defined, these individuals were always associated with groups of muskoxen.

I identified changes in the seasonal distribution of the muskox population by comparing adaptive-kernel contours generated from locations of all muskox groups observed during seasonal radio relocation surveys in 1982-95. Data for all years were combined. I determined seasonal shifts of individual females by measuring the distance (km) between the centers of core areas and the amount of overlap (km²) between core areas defined for satellite-collared muskoxen in different seasons. Measurements were made using the ARC/INFO (ESRI, Redondo, CA) geographic information system (GIS).

Movement and Activity

I calculated mean movement rates (km/day) for each season and each month from distances moved by satellite-collared muskoxen between consecutive locations at 40-55 h intervals. Activity counters in satellite-collars recorded numbers of tip-switch

closures at 1-second intervals during a 24-h period (Fancy et al. 1988). Observations of captive muskoxen carrying satellite collars showed that active and resting behavior could be distinguished by number of tip-switch counts (D. R. Klein, et al. 1987. Testing a calibration of activity-monitoring satellite-collars on captive muskoxen, unpublished report, 2nd International Muskox Symposium, Saskatoon, Saskatchewan, Canada). I used activity counts from 5 satellite-collared muskoxen that had > 10 days of activity counts per month. I divided 24-h activity counts by 1440 to determine counts per minute and calculated a mean index of activity for each season and each month.

Seasonal differences in overlap of core areas used by satellite-collared females, distances between core-area centers, core-area size, movement rates, and activity indices were tested with analysis of variance (ANOVA) followed by Tukey's Studentized range test (SAS Institute Inc. 1985). Differences were considered significant at $P < 0.05$.

Habitat Use

I used land-cover and terrain types from a land-cover map derived from LANDSAT/TM data (Jorgenson et al. 1994) to determine seasonal differences in habitat use. I calculated total area (km²) and proportions for each of 6 land-cover classes (wet sedge, moist sedge, tussocks, upland shrub, riparian vegetation, water-bare ground) and 5 terrain types (river corridor, flood plain, foothills, hilly coastal plain, thaw lake plain, mountains) that occurred within core areas used seasonally by satellite-collared muskoxen. Both land cover and terrain type are important to understanding seasonal use of landscapes (Nelleman and Reynolds 1997). The land-cover map had an accuracy of 70% for the 6 land-cover classes used (J. Jorgenson, USFWS Arctic NWR, unpubl. data). I used proportions of land-cover and terrain classes within the entire study area (Jorgenson et al. 1994) as a measure of availability of these habitats.

I calculated selection ratios (w_i) (Manly et al. 1993) for each land-cover and terrain type in each season by dividing the proportion of the type in all core areas combined by the proportion occurring in the entire study area (use/availability). I defined selection of a cover or terrain type as $w_i > 1.0$, use in proportion to availability as $w_i = 1.0$, and avoidance as $w_i < 1.0$.

RESULTS

Size of Seasonal Use Areas

The size of core areas defined for satellite-collared muskoxen differed among seasons ($F_{4,112} = 16.58$, $P = 0.0001$) (Table 5). Core areas were significantly larger in summer ($P < 0.05$), on the average, almost an order of magnitude larger than ranges used in mid- and late winter (Table 5). The minimum size of core areas used in summer by satellite collared muskoxen was more than four times larger than the minimum size of core areas occupied in early, mid- or late winter (Table 5).

Seasonal Movements and Activity

Muskoxen were conservative in their daily movements throughout the year, moving only short distances during the course of daily cycles of feeding and resting. Ninety five percent of 2314 movements made by satellite-collared muskoxen were at rates < 5 km/day (Table 6). Of these, 46% were < 1 km/day.

Animals moved at rates of 5-10 km/day in $< 5\%$ of 2314 movements (Table 6). Such movements were along rivers or between adjacent drainages as animals moved between feeding sites. Seventy one percent of 108 movements at rates of 5-10 km/day occurred in summer (Table 6).

Movement rates of > 10 km/day were rare (18 of 2314 movements, Table 6). These higher rates of movement were associated with shifts between seasonally used regions or dispersal into new regions (Chapter 3). Sixteen (89%) of movements > 10 km/day occurred during summer and all of these took place during July.

Movement rates differed by season ($F_{4, 2309} = 59.05$, $P = 0.001$). Female muskoxen made greater daily movements in summer than in other seasons ($P = 0.05$) (Table 6). Mean rates of movement also differed among months ($F_{11, 2309} = 32.58$, $P = 0.001$) and were significantly higher ($P < 0.05$) in July than in all other months (Fig. 6).

Activity indices also differed by season ($F_{4, 1370} = 114.96$, $P < 0.001$) and were more active in summer than in other seasons ($P < 0.05$) (Table 6). Activity indices differed among months ($F_{11, 1370} = 32.58$, $P = 0.001$) and were highest in July and lowest in April, at the onset of the calving season (Fig. 6).

Seasonal Shifts in Distribution

Mean distances between seasonal home ranges, measured from the center of the ranges, were longest between ranges used in calving and summer seasons and shortest between ranges used in mid- and late winter (Table 7). Maximum distances between seasonal ranges were 28 km (mid-to late winter) to 114 km (calving to summer).

Seasonal home ranges occupied by female muskoxen overlapped less ($F_{4, 109} = 3.41$, $P = 0.01$) between calving and summer than between early winter and mid-winter, and mid-winter and late winter (Table 7). Overlap of seasonal core areas was not significantly different ($F_{4, 109} = 1.34$, $P = 0.26$) because of high variability between individuals (Table 7).

Twenty three of 37 radio-collared females followed for at least 3 years made movements outside of seasonal home ranges, but only 8 of these females made these seasonal movements in ≥ 2 years, and no marked females made seasonal movements every year that they were observed. The population of muskoxen in the Arctic NWR, which was generally concentrated in 3 geographic regions (Ch. 1. Fig. 4), showed little change in distribution between seasons (Fig. 7).

Seasonal Shifts in Habitat Use

Female muskoxen selected riparian cover in all seasons, but selection ratios for this cover type were higher in winter than during calving or summer (Fig. 8). In addition, moist sedge was selected in late winter and calving, tussock tundra was avoided in late winter, but these cover types were used in proportion to availability the remainder of the year. Wet sedge was avoided in all seasons except summer and early winter when it was used in proportion to availability. Upland shrub was avoided in all seasons except in calving when it was selected (Fig. 8).

Bare cover (which included bare ground, water and ice) was selected in all seasons except spring (Fig. 8). This high use of areas containing little or no vegetation reflected the proximity of this cover type to riparian communities along river corridors and flood plains that also included wide river channels and gravel bars with sparse vegetation.

River corridors, flood plains adjacent to river corridors, and foothills were terrain types selected in all seasons (Fig. 8). Selection of foothills was highest during the calving season. Hilly coastal plains were strongly selected in summer but avoided in mid-winter. Thaw-lake plains were avoided in calving and summer, but selected in mid- to late winter. Mountains were strongly avoided in all seasons (Fig 8).

DISCUSSION

Muskoxen showed little seasonal change in spatial distribution. Seasonal ranges used by satellite-collared females in calving, summer and winter were separated by 20-30 km, on the average. But seasonal ranges had a high percentage of overlap and most drainages used by muskoxen were occupied in all seasons. Few long distance movements were evident in any season. The large overlap in seasonal distribution of the muskox population in northeastern Alaska as well as low rates of movement by individuals confirm that, in general, female muskoxen are energetically conservative

throughout the year (Jingfors 1980, Thing et al. 1987) and have a high fidelity to geographic regions.

Seasonal changes in habitat use were related to seasonal availability of vegetation. Snow limits forage availability and influences winter habitat selection by muskoxen (Jingfors 1980). In winter, muskoxen select feeding sites in areas with shallow soft snow (Biddlecomb 1992, Wilson 1992). By mid- and late winter, riparian willows may be covered by deep snow (Wilson 1992). Wet-sedge communities also may be less available in winter and calving compared with summer due to deep snow (Evans et al. 1989). Selection of river corridors in winter includes the use of narrow windblown bluffs adjacent to rivers (Nellemann and Reynolds 1997). The increased use of foothill terrain and upland shrub by muskoxen during the calving season reflects shifts into areas where snow cover likely is shallow or blown free. Muskoxen with young calves also may avoid flooded riparian areas during calving and post-calving periods. During the snow-free period in summer, muskoxen forage on a wide variety of high-quality vegetation (Robus 1981, O'Brien 1988).

Forage accessible to muskoxen in winter and spring is of low quality (Staal and Olesen 1992). Dried graminoids are a dominant component of the late winter diet of muskoxen in northeastern Alaska (Biddlecomb 1992, Wilson 1992, O'Brien 1988), Greenland (Thing, et al. 1987; Klein and Bay 1990) and Canada (Parker 1978). Muskoxen have a large body size and rumen, with a low rate of food passage that allows digestion of graminoids with a high fiber content (Klein 1992). Efficient digestion of low quality forage and relatively low metabolic requirements (Adamczewski et al. 1994) help muskoxen to maintain body condition throughout winter and spring (Thing et al. 1987).

Seasonal changes of movement rates and activity of muskoxen are strategies related to energy input and conservation. Movement rates and activity increase in June at the onset of annual green-up, are highest in July as live biomass peaks (Chapin

1983), and begin to decline in August as plant senescence and rut occurs. In northeastern Greenland, the percent of time muskoxen spent feeding increased through the growing season and peaked in July (Olesen 1987). In western Greenland, Forchhammer (1995) found a decrease in both rumination time and daily feeding time as forage quality increased and speculated that, by contrast, muskoxen in northeastern Greenland were subjected to more severe winter conditions and increased foraging time to maximize forage intake in summer. Increased movements in summer also may be related to: insect harassment or warm weather (Jingfors and Klein 1982), to incidents of predation by brown bears (Clarkson and Liepins 1993), or to social behavior associated with the breeding season in August and early September.

The reductions in movements and activity in winter may be related to forage quality and energy conservation not measured in this study. Long resting periods in winter are required for digestion of low quality forage (Jingfors and Klein 1982). In western Greenland, rumination time increased in winter as animals digested poorer quality forage (Forchhammer 1995). In northeastern Greenland, percent time lying was highest and percent feeding time was lowest in February, and the length of resting periods were longer in winter and calving than in summer (Olesen 1987).

Maier et. al (1996) reported that ambient air temperature affected activity counters on radio collars, indicating that lower counts in winter may not necessarily reflect decreases in animal activity. In this study, the positive correlation of activity counts with movement rates and the fact that activity was lowest in April during calving rather than during the coldest months of January and February indicate that the seasonal differences observed in this study reflected seasonal changes in animal behavior.

In this study, female muskoxen had low levels of activity and low movement rates in April at the onset of the time when calves were born. Many ungulates, including caribou, reproduce when highly nutritious vegetation is emerging. By

contrast, muskox calves are born when winter conditions still prevail in northeastern Alaska. Lactating females must subsist on winter forage and move through snow for several weeks after the birth of a calf, and conservation of energy is critical during that period. Similar conditions exist for Dall sheep (*Ovis dalli*) in central Alaska (Rachlow and Bowyer 1994).

Seasonal shifts in distribution and behavior reflect a balance between energy intake and energy expenditures (White et al. 1981, Klein 1986). In summer, muskoxen occupy larger areas, move longer distances, and are more active to take advantage of seasonally abundant forage (Klein and Bay 1990) and to exploit changing plant phenology in different areas (Guthrie 1984). By this means, females increase their intake of energy and other nutrients to provide milk for a growing calf and to regain body weight lost during winter, pregnancy, and lactation. Muskoxen in Greenland also use an energy-maximizing strategy in summer (Forchhammer 1995). The most rapid weight gain in female muskoxen occurs in late summer during the breeding period in August and September (Adamczewski et al. 1992, White et al. 1997), when lactating animals also decrease milk output (White et al. 1989).

The strategy of muskoxen in winter and calving seasons is to conserve energy. Muskoxen are adapted to the cold weather with their stocky bodies, short legs, and thermally efficient pelage (Klein 1992). Cratering for food through deep snow and moving between foraging patches is energetically costly for muskoxen. By reducing movements and activity, decreasing the size of use areas, and selecting habitat types where forage is not covered with deep snow, muskoxen minimize energy expenditures.

The shift in seasonal strategies from maximizing energy intake in summer to energy conservation in winter and calving, as well as adaptations for cold weather and the ability to process low quality forage, allows muskoxen to survive year-round in an area seasonally avoided by most other animals.

MANAGEMENT APPLICATIONS

In northern Alaska, human presence is increasing, as are pressures to open areas for exploration and extraction of natural resources, including oil and gas. Human activities, including hunting and resource extraction, that increase energetic costs to muskoxen in winter and calving seasons through disturbance, or decrease forage availability in summer through habitat loss or lack of access to habitats, have the greatest probability of affecting muskoxen in the Arctic NWR. Riparian habitats that are heavily used by muskoxen are also winter transportation corridors for snow machines and are potential sites for gravel and water extraction and winter roads if development of petroleum resources occurs on the coastal plain of the Arctic NWR.

Many exploratory and developmental activities in northern Alaska take place in winter to minimize impacts on tundra underlain by permafrost and to avoid calving caribou. However, conducting development activities in winter months will result in conflicts with muskoxen because these animals are year-round residents on the Arctic NWR, have limited access to winter forage, and must conserve energy in winter.

Minimizing human activities in areas occupied by muskoxen from mid-winter through the calving period in April and May would reduce the likelihood of disturbance during the period when energy conservation is critical. The siting of permanent or semi-permanent facilities away from known areas of muskox occupation along river corridors and flood plains would also help reduce potential impacts on muskoxen.

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Table 4. Biological and ecological factors associated with seasons used in an analysis of seasonal changes in distribution, habitat use, movements and activity patterns in a population of muskoxen in northeastern Alaska.

Season	Calving			Summer			Early winter		Mid-winter		Late winter		
Month	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar
Births		+	+	+	+	+							
Sunlight ^a	12	21	24	24	24	21	12	6	0	0	0	6	8
Forage ^b					+	+	+	+	+				
Mating						+	+	+	+	+			
Snow	+	+	+	+	+	+	+	+	+	+	+	+	+
Temp C ^o	-25	-19	-5	+2	+6	+6	0	-10	-20	-22	-26	-26	-23

^aNumber of hours per day that the sun is above the horizon

^bPeriod of plant growth

Table 5. Size of core areas (km²) used seasonally by satellite-collared female muskoxen in northeastern Alaska, 1986-92. Core areas were defined for individuals from 70% adaptive kernel contours of satellite locations in each season.

Season	<i>n</i>	Minimum	Maximum	\bar{x}	SD	
Calving	24	5	59	28	13.4	A ^a
Summer	28	39	806	223	204.7	B
Early winter	24	9	260	70	70.0	A
Mid winter	22	8	134	31	25.9	A
Late winter	19	2	91	27	19.8	A

^a Different letters indicate significant differences within a column ($P < 0.05$, Tukey's Studentized range test, following ANOVA).

Table 6. Seasonal patterns of movement and activity of female satellite-collared muskoxen in northeastern Alaska, 1986-92.

Season	Number of moves in each rate category						Activity index (counts per minute)				
	(km per day)			Movement rate (km per day)							
	< 5	5-10	> 10	<i>n</i>	\bar{x}	SD					
							<i>n</i>	\bar{x}	SD		
Calving	559	9	0	568	1.1	1.0	A	347	11	6.5	A
Summer	568	77	16	661	2.6	3.1	B	430	19	8.8	B
Early winter	363	13	2	378	1.6	1.6	CD	284	9	5.3	C
Mid-winter	430	8	0	438	1.4	1.2	AD	183	12	4.9	A
Late winter	268	1	0	269	1.2	1.0	AD	141	11	4.0	AC

^a Different letters indicate significant differences within a column ($P = 0.05$, Tukey's Studentized range test following ANOVA).

Table 7. Mean distances and overlap between home ranges used in different seasons by satellite-collared female muskoxen in northeastern Alaska, 1986-92. Total home range and core areas were defined using 95% and 70% adaptive-kernel contours, respectively. All females were associated with mixed-sex groups.

Comparisons between ranges used seasonally	<i>n</i>	Distance (km)								
		between centers ^a of ranges used				Percent overlap between ranges				
						seasonally		Total range		Core area
		<i>̄x</i>	SD			<i>̄x</i>	SD		<i>̄x</i>	SD
Calving to summer	23	32	29	A ^b	41	39	A	21	35	A
Summer to early winter	26	21	15	B	52	38	AB	22	34	A
Early winter to mid-winter	24	16	15	BC	71	33	B	30	35	A
Mid-winter to late winter	21	6	6	D	72	28	B	39	33	A
Late winter to calving	26	10	15	CD	52	32	AB	29	31	A

^a Center of 5% adaptive kernel contour

^b Different letters indicate significant differences within a column ($P < 0.05$, Tukey's Studentized range test, following ANOVA).

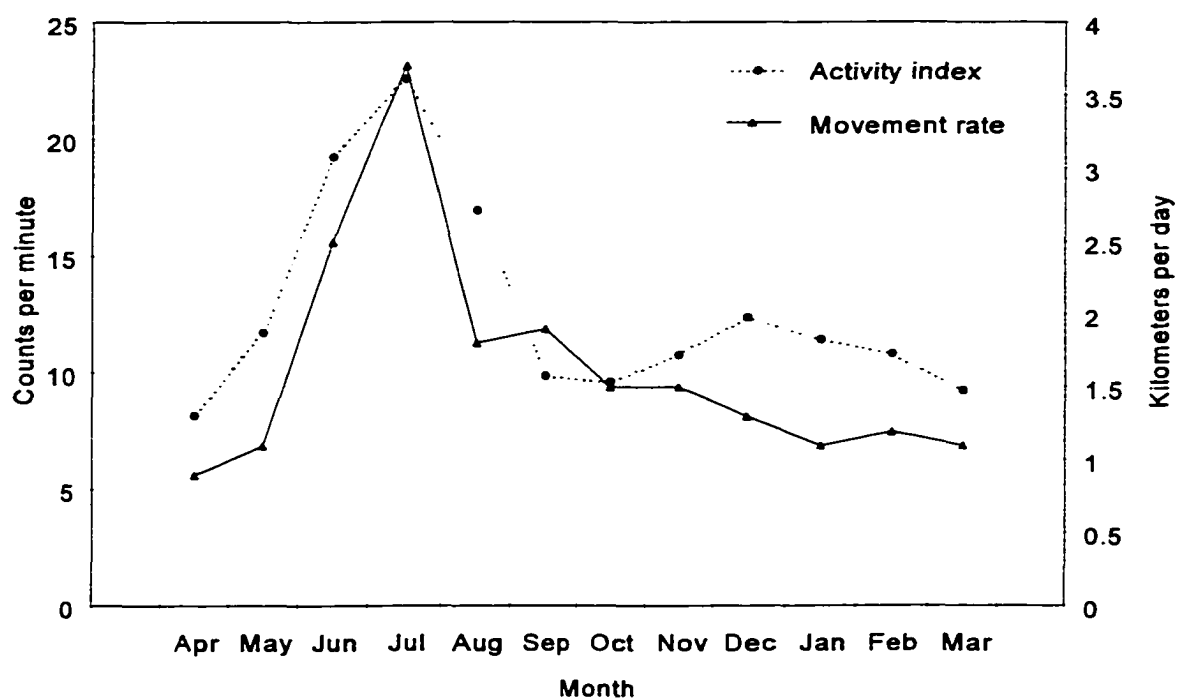


Fig.6. Mean movement rates and mean activity indices from satellite-collared female muskoxen in northeastern Alaska, 1986-1992.

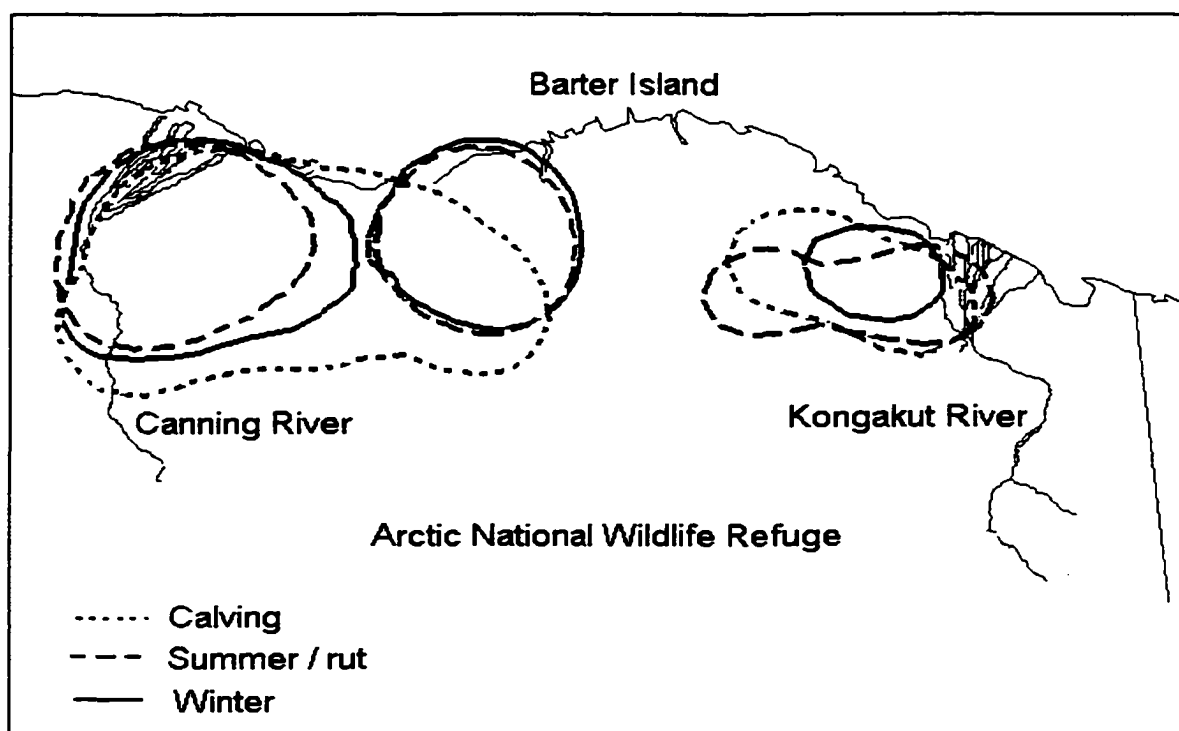


Fig.7. Muskox population distribution during different seasons in the Arctic National Wildlife Refuge in northeastern Alaska, 1982-95. Distribution was based on 70% adaptive-kernel contours generated from locations of muskox groups seen during radio-relocation surveys in calving (March and May), summer (June and August), and winter (October and February) seasons.

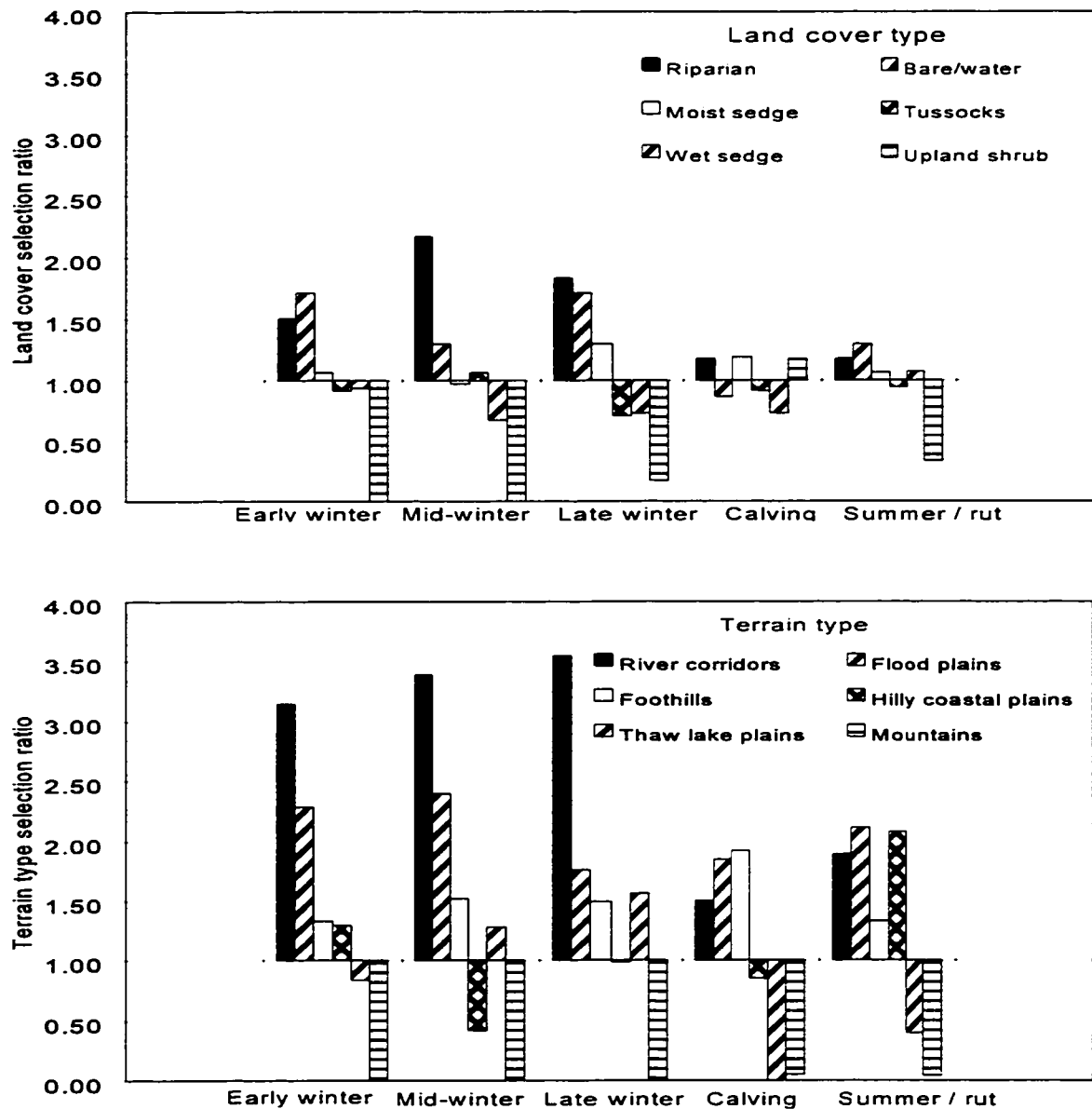


Fig. 8. Seasonal use of different land cover and terrain types in home range core areas (70% adaptive kernel contours) occupied by satellite-collared female muskoxen in northeastern Alaska.

CHAPTER 3.

DISPERSAL OF MIXED-SEX GROUPS IN AN EXPANDING POPULATION OF MUSKOXEN

ABSTRACT

Dispersal of animals into new ranges is a critical component of the dynamics of expanding populations. I studied dispersal of mixed-sex groups in a reestablished population of muskoxen (*Ovibos moschatus*) in northeastern Alaska. I used locations of satellite-collared females and muskox groups observed during telemetry surveys, annual population censuses, and ground composition counts to identify attributes associated with dispersal events and shifts in distribution that resulted in range expansion. Attributes included direction, timing and scale of dispersal, size and stability of dispersing groups, age and reproductive status of dispersing females, and trends in production of calves, survival of calves and yearlings, and the size of mixed-sex groups. I used these observed attributes to test predictions about models that may explain the process of dispersal in an expanding population. Dispersal of female muskoxen in mixed-sex groups occurred infrequently as most females were philopatric and rarely made long movements outside established home ranges. Dispersal of mixed-sex groups was not a process of diffusion; mixed-sex groups moved into new ranges through periodic pulses of dispersal that occurred primarily during mid- or late summer (rut). Both density dependent and density independent factors influenced the dispersal of mixed-sex groups of muskoxen. Habitat change resulting from increasing animal densities likely contributed to the initial pulse of dispersal from regions first occupied. Social factors associated with increasing densities and weather conditions (cold short summers and winters of deep snow) that affected the annual availability of forage also were related to the dispersal of mixed-sex groups.

INTRODUCTION

Spatial and temporal shifts in animal distribution are important components in the dynamics of expanding populations and are means by which populations spread into unoccupied ranges. Dispersal of animals, mating systems, and demography play a key role in determining the genetic structure of a population, which has consequences for social behavior, population dynamics, and evolution (Shields 1987). Dispersal is one mechanism by which a population copes with changes in habitat availability (Caughley 1977).

Dispersal has been defined as a one-way movement outside of a home range (Stenseth and Lidicker 1992), as emigration from one home range to another (Holekamp and Sherman 1989), and as movement from where an animal is born to where it reproduces (Howard 1960). In this study, I defined dispersal as a population process resulting in range expansion, and defined dispersal events as a series of movements by individuals in social groups that resulted in emigration into new home ranges.

Proximate causes of dispersal, including competition for resources, competition for mates and avoidance of inbreeding have been addressed in many studies, primarily in small mammals (Gaines and McClenaghan 1980, Swingland and Greenwood 1983, Chepko-Sade and Halpin 1987, and Stenseth and Lidicker 1992). Dispersal of large mammals occurs on a different habitat scale, plays a less important role in limiting density, and is considered to be adaptive (Sinclair 1992). Muskoxen (*Ovibos moschatus*), extirpated from Alaska in the 1800's, were reestablished in northeastern Alaska in 1969-79 (Chapter 1). This restored population provided an opportunity to study the role of dispersal in a population of large mammals expanding into regions of former range.

Because range expansion of a species requires dispersal of reproducing animals into new or formerly occupied regions, this study focused on the dispersal of mixed-sex

groups, which contained females, young-aged animals, and often one or more adult males. The dispersal of male muskoxen, described by Smith (1989), was addressed only briefly in this study. Male muskoxen inhabit much larger home ranges than females and disperse more frequently, but do not reproduce unless they return to regions occupied by mixed-sex groups (P. E. Reynolds, unpublished data).

In a population where animal densities are increasing, several factors may be involved in dispersal and range expansion. I propose four models that may explain the process of dispersal of mixed-sex groups in this reestablished population of muskoxen. To test these models, I made predictions about attributes associated with dispersal events and shifts in population distribution resulting in range expansion (Table 8). These models were not assumed to be mutually exclusive; dispersal is a complex process, likely involving more than one factor (Lidicker and Stenseth 1992).

Dispersal in this population of muskoxen may be a process of simple diffusion in which animals disperse continuously in random directions (Caughley 1977). If mixed-sex groups in this muskox population dispersed via diffusion, I predicted that numbers of muskoxen in regions first occupied would be positively correlated with the size of areas occupied by mixed-sex groups. I also predicted that range expansion of the population would occur in all directions, that mixed-sex groups would disperse continuously in all directions, and that dispersal would take place in all seasons (Table 8).

Dispersal of mixed-sex groups may be a density-dependent process. Weather conditions in Arctic Alaska are variable from year to year and affect forage availability, animal survival and production of young. In northeastern Alaska, the growing season for plants is only 6 to 8 weeks, and most forage available to muskoxen during the remainder of the year is the product of this brief period of plant production. Snow covers the ground for 8-9 months each year. Annual variability in weather influenced reproduction and survival of muskoxen in Canada (Gunn et al. 1989, Gray

1987). Severe weather conditions including deep snow or icing may force muskoxen to move in search of forage or find relief from local environmental conditions. If weather in summer results in poor production of plants, muskoxen may need to range over larger areas to acquire adequate nutrition to replace body reserves lost during the previous winter and calving season. In addition, effects of weather may be exacerbated at high population densities. If weather conditions were a major factor in the dispersal of mixed-sex groups in this population, I predicted that pulses of dispersal would be related to weather events that affect plant production (e.g. short cold summers) or influence access to forage and the energetic costs of obtaining food (e.g. long winters with deep snow) (Table 8). I also predicted that females in mixed-sex groups influenced by weather conditions would disperse in late winter when snow reached a maximum, or in mid-summer when forage biomass peaked (Chapin 1983) and that dispersal would take place on a regional scale (i.e. multiple events from different locations during the same season and year).

Dispersal in an expanding population also may be a density-dependent process. As densities of muskoxen increase over time, the population may approach or exceed carrying capacity (K), resulting in damage to forage resources and intraspecific competition for food. Under these conditions, saturation dispersal occurs as some animals are forced to disperse to survive (Lidicker 1975). Depleted habitats reduce the ability of female muskoxen to reach the minimum body mass needed to ovulate, breed, and successfully carry a pregnancy to term (White et al. 1989) and may increase the time between successful reproductive events. The size of mixed-sex groups in summer may also decline as habitat productivity decreases (White et al. 1981). If mixed-sex groups dispersed because of habitat change, I predicted that group size, calf production, and survival rates would decrease during the years before dispersal first occurred and that dispersal events would take place during May or early June when

nutritional needs of lactating females approached an annual peak and the summer growing season had not commenced (Table 8).

Mixed-sex groups under conditions of increasing densities may also disperse before negative effects on forage occur, for example, when densities reach a social threshold. This type of dispersal was described as pre-saturation dispersal (Lidicker 1975, Stenseth and Lidicker 1992). In highly gregarious species, social hierarchies result in the exclusion of subordinate animals from access to adequate forage or prospective mates (Sinclair 1977, Clutton-Brock and Albon 1985). Under conditions of high density and stressful social interactions, mixed-sex groups of muskoxen may split into smaller units with some animals moving long distances into new ranges. If social factors were a primary cause of dispersal of mixed-sex groups, I predicted that mean group size would increase in the years before the first dispersal of mixed-sex groups, and that dispersing groups would be unstable (e.g. group size would change) during the process of dispersal. I also predicted that dispersal events would take place in mid to late summer (Table 8). The mating season (rut) for muskoxen in northeastern Alaska occurs in August and September and social interactions in this polygynous species are at a maximum during that time of year (Gray 1987).

STUDY AREA

The study area, between the Sagavanirktok River (148.7° E) in Arctic Alaska near the oil fields at Prudhoe Bay, and the Clarence River (141.0° E) on the U.S.-Canada border is bounded on the north by the Arctic Ocean (Beaufort Sea; 70.2° N), and on the south by the mountains of the Brooks Range (69.3° N) (Fig. 1). This area (24,700 km²) encompasses the coastal plain of the Arctic National Wildlife Refuge (Arctic NWR). The land is underlain by continuous permafrost and is snow-covered for 8-9 months. Vegetation is arctic tundra: shrubs (*Salix*), forbs (*Hedysarum*, *Lupinus*), and graminoids grow on partially vegetated gravel bars of rivers; tussock-

shrub (*Eriophorum*, *Betula*), low shrub (*Betula*, *Salix*), and shrub-heath communities (*Carex*, *Dryas*) occur on the slopes of adjacent rolling hills, and sedge-moss communities (*Carex*, *Drepanocladus*) dominate flat poorly drained areas (Bliss 1981). Major features of terrain include braided north-flowing rivers and flood plains, foothills, hilly coastal plains, thaw-lake plains, and mountains (Walker et al. 1983).

METHODS

Attributes associated with dispersal events and range expansion.

Radio and satellite telemetry. I used very-high frequency (VHF) radio-collars relocated by fixed-wing aircraft, and platform terminal transmitters (PTT's) located by satellite (satellite collars) on adult muskoxen to determine changes in population distribution over time and to document home-range occupation and movements. Muskoxen to be collared were immobilized with Carfentanyl citrate (WILDNIL™, Janssen Pharmaceutical) and xylazine (ROMPUN™, Mobay Corp.) administered from projectile syringes fired from helicopters.

I maintained 19 to 25 radio-collared muskoxen in the population each year from 1983-1995 to assist in locating mixed-sex groups and to determine reproductive rates of individual females over time. I relocated radio-collared muskoxen during 4- 6 surveys each year in all seasons by flying along major drainages and recording locations of mixed-sex groups (both marked and unmarked) using a Global Positioning System (GPS) mounted in the aircraft, or on 1:63360 scale maps accurate to the nearest 0.5 km. I also recorded group size, number of calves and number of marked individuals in each group. Each year from 1987 to 1992, 3-8 of these radio-collared animals also carried satellite collars that were located every 2 to 3 days.

Population distribution, home ranges and dispersal events. The study area was subdivided into regions first occupied by muskoxen released near the Arctic NWR and regions into which muskoxen later dispersed (regions occupied later) (Chapter 1,

Fig. 1). I used an adaptive-kernel technique (Worton 1989; program CALHOME; Kie et al. 1996) to delineate changes in population distribution over time. I used locations of mixed-sex groups of muskoxen obtained during radio-relocation surveys to determine population distribution during 1983-95. The distribution of the muskox population in 1969-81 was based on locations of muskox groups seen during annual surveys and other studies of wildlife (Roseneau and Warbelow 1974, D. Ross, Arctic NWR unpubl. data). I used the adaptive-kernel technique to define home ranges of 37 radio-collared females followed for at least 3 consecutive years between 1982 and 1995. With rare exceptions, female muskoxen are always associated with mixed-sex groups of muskoxen. Therefore, delineated home ranges were ranges occupied by groups of animals, not solitary individuals. But because mixed-sex groups of muskoxen often split into smaller units or merge with other groups (Reynolds 1993), I could not follow identifiable groups of animals through time.

The adaptive-kernel technique assumes independence of data points. Locations observed during radio-relocation surveys were not significantly autocorrelated ($P > 0.10$), based on the results of multi response sequence procedure tests (program BLOSSOM; Slauson et al. 1991). I used the 70% adaptive-kernel contour to define core areas used by radio-collared females and areas of population concentration occupied by mixed-sex groups and the 95% adaptive-kernel contour to delineate home range boundaries and the maximum extent of distribution of mixed-sex groups. I used distances between consecutive locations of radio-collared muskoxen to identify movements > 29 km. From these long moves, I identified events associated with temporary and permanent movements from home ranges. I defined seasonal and exploratory events as temporary two-way movements from and back to the same home ranges while dispersal events were defined as from one-way movements into new home ranges.

Timing, distance and direction. To identify pulses of dispersal of mixed-sex groups that resulted in range expansion through the occupation of new regions, I compared numbers of muskoxen in mixed-sex groups seen during annual censuses in regions first occupied with numbers in regions occupied later. Years when shifts between these regions took place were years when pulses of dispersal occurred. I also identified years and seasons in which radio-collared females in mixed-sex groups made movements that resulted in dispersal events and determined the proximity of new home ranges to original home ranges. I calculated rates of movement and actual dates of dispersal for muskoxen carrying satellite-collars. I used temperatures from Barter Island (1982-1988) and Prudhoe Bay (1989-1995) (National Oceanic and Administration, Barter Island, Alaska, National Climatic Data Center, Asheville, North Carolina) and snow depth from measurements made at a foothills site 90 km west of the study area (Kane 1997) to examine weather conditions from 1983 to 1995. I used correlation and a binomial test (Zar 1984, p 321, 383) to compare years when adverse weather conditions and pulses of dispersal did and did not occur together.

I determined the initial direction moved by dispersing female muskoxen. I also calculated the relative distance between the furthest north and south locations, and east and west locations of mixed-sex groups observed in 1982-1985, before dispersal of mixed-sex groups began, and in 1986-1995 after dispersal had commenced. I correlated muskox abundance in regions first occupied with the size (km^2) of regions occupied by mixed-sex groups (70% adaptive kernel contour) to determine if mixed-sex groups expanded their range continuously in all directions. I used chi-square tests to test the goodness-of-fit of directional and seasonal data to a theoretical circular frequency distribution (Zar 1984, p 441).

Group size, age, productivity and survival. I calculated the average size of mixed-sex groups by year, compared the average size of mixed-sex groups in regions

first occupied with regions occupied later, and determined changes in mean group size and numbers of radio-collared animals within a group before and after dispersal events.

I estimated ages of marked females as 2 years, 3 years, young adult (about 4-6 years), mature adult (about 7-10 years), or old adult (> 10 years) based on the wear of the teeth, and the color and size of the horns. I estimated minimum birth years from these age classes (e.g. a female classified as a young adult in 1985 was assumed to be born in 1981) and compared the mean birth years of dispersing and nondispersing females. I determined the reproductive status of marked females from ground observations and calculated a reproductive index (no. calves/no. of years observed) to compare dispersing and nondispersing females.

I used ratios of calves:100 cows > 2 years old as a measure of calf production. I estimated calf and yearling survival from estimates of calves, yearlings and 2- year-olds in the population in consecutive years. These estimates were based on numbers in these age classes per 100 females > 2 years at time of their birth (Chapter 1). I determined changes in productivity of calves and survivorship of calves and yearlings over time using linear regression, and correlated annual trends in production and survival in regions first occupied (PROC CORR, SAS Institute Inc. 1985). I compared mean calf production in regions first occupied and regions occupied later. I used t -tests (PROC TTEST, SAS Institute Inc. 1985) to test differences in group size, reproductive indices and calf production in different regions ($\alpha = 0.05$).

RESULTS

Description of spatial events

Female muskoxen in this expanding population rarely dispersed. Most had high fidelity to home ranges and were conservative in their movements. Eighty-three percent of 983 movements defined from consecutive locations of radio-collared females were inside home ranges, and 76% of these 828 inter-home range movements

were of short (< 10 km) or medium distance (10-29 km). Long- distance movements (> 29 km) within home ranges occurred infrequently and were primarily related to seasonal shifts (7% of 828 movements). Movement rates calculated from consecutive locations of satellite-collared females averaged 1.7 km/d ($n = 2314$ movements); only 1% ($n = 27$) were > 20 km/d. Movements outside of home ranges happened infrequently (16% of 983 movements) and were associated with 3 types of spatial events: seasonal events, transitory events, and dispersal events. Each event consisted of ≥ 1 long distance movements made by a radio-collared female in a mixed-sex group. Seasonal events occurred when females in mixed-sex groups moved between 2 seasonally used ranges, or temporarily moved from a home range, but returned in 3- 8 months. Seventy-six percent of 155 movements related to events outside of home ranges were associated with seasonal events.

Transitory events occurred when females in mixed-sex groups moved from their home ranges, but eventually returned to those home ranges after ≥ 1 year. Like seasonal events, transitory events were composed of an outward movement and a return movement, but because of their extent, transitory events were interpreted to be exploratory movements or temporary dispersal.

Dispersal events occurred when females in mixed-sex groups made one-way movements from existing home ranges and established new home ranges in previously unoccupied regions. Eighty-eight percent of 25 movements associated with dispersal events were > 49 km. Dispersal and transitory events occurred infrequently; I identified only 13 dispersal events and 5 transitory events from 1982 to 1995.

Twenty of 37 radio-collared females were highly philopatric nondispersers, living in the same home range throughout the study, 6 females used transitory events to temporarily occupy more than one home range or several cores within a large home range, and 11 muskoxen permanently dispersed and occupied 2 or more different home ranges. Five of 6 females making transitory movements and 9 of 11 dispersing

females also made seasonal movements outside of home ranges, compared with 9 of 20 nondispersing females. Two individuals dispersed twice.

Attributes associated with dispersal events and range expansion.

Dispersal interval. Dispersal of mixed-sex groups was not a continuous process but took place at intermittent intervals. In 1985 and 1986, 2 small (3-9) mixed-sex groups were observed east and west of regions first occupied. Large pulses of dispersal of mixed-sex groups from regions first occupied occurred periodically, with the first pulse taking place between 1986 and 1987 (Fig 9). In 1986, radio-collared females in 2 different mixed-sex groups dispersed westward from these regions during summer (Fig.10). Other major pulses of dispersal from regions first occupied occurred between 1988-89, 1991-92, and 1994-95 (Fig.9). The largest number of dispersal events (46% of 13 events) took place in 1988 and 1989 and large proportions of outward movements associated with transitory events (40% of 5) and seasonal events (30% of 56) also occurred during these years (Fig. 11). Shifts in population distribution and dispersal events resulting from movements of radio-collared females indicated that muskoxen moved back into regions first occupied between 1992 and 1993 (Fig. 9, Fig. 10).

Direction. Numbers of muskoxen in regions first occupied were not correlated ($r = -0.20$, $P = 0.51$) with the size (km^2) of mixed-sex areas of concentration (based on the 70% adaptive kernel contour) indicating that mixed-sex groups did not disperse continuously in all directions. Directions of outward movements associated with dispersal and transitory events were not in all directions ($X^2 = 54.9$, $P < 0.001$). Dispersing females in mixed-sex groups moved primarily east and west (Fig. 12). Movements associated with seasonal events were also directional ($X^2 = 54.9$, $P < 0.001$), but 34% of these movements were north or south and 43% were east or west (Fig.12). Population shifts in the distribution of mixed-sex groups of muskoxen also indicated that mixed-sex groups of muskoxen dispersed along an east-west axis

(Chapter 1, Fig.4). In 1986-89, maximum north and south locations were only 8 km and 4 km, respectively, beyond maximum north and south locations observed in 1982-85. In 1986-89, however, maximum locations were 76 and 51 km further east and west, respectively, than in 1982-85. The presence of the Beaufort Sea to the north and the rugged mountains of the Brooks Range to the south likely influenced directional movements of mixed-sex groups.

Season and weather. Dispersal events did not occur in all seasons ($\chi^2 = 34.3$, $P < 0.001$). All but 2 dispersal events ($n = 13$) and all outward transitory events ($n = 5$) were initiated during summer (late June to mid-September) (Fig.13). By contrast, outward seasonal events ($n = 56$) occurred during calving (late March to mid-June) (46%), summer (25%) and early winter (late September to mid-November) (25%) with animals returning primarily in summer (59%) or early winter (20%). One radio-collared female dispersed between June 11 and July 2, and 3 satellite-collared females dispersed in July (Table 9). Movements of satellite-collared muskoxen showed that the long moves initiating dispersal events occurred rapidly, over a maximum of 2-3 days rather than over several weeks (Table 9).

Years in which pulses of dispersal out of regions first occupied took place were significantly correlated ($r = 0.57$, $P = 0.03$) with years of low temperatures in July and deep snow the following winter (Fig. 14). During these years, July temperatures were 1- 2° C below the 1986-1996 mean (6.4° C), and averaged 4.7° C compared with an average of 7.3° C in years after 1986 in which animals did not disperse. July temperatures were negatively correlated ($r = 0.62$, $P = 0.04$) with snow depth the following winter. The cold summers in which muskoxen dispersed were characterized by an early onset of winter weather as indicated by heavy snowfall in August or early September and/or below normal temperatures in August.

Distance and scale. In 8 dispersal events, radio-collared females in mixed-sex groups moved into regions adjacent to their first home ranges. In 5 events, females

moved through regions already occupied by mixed-sex groups into nonadjacent regions. All 5 transitory events were between adjacent regions .

Although dispersal events were likely influenced by local conditions, multiple dispersal events took place in 1986, 1988 and 1989 (Fig. 10) indicating the dispersal of mixed-sex groups occurred on a regional scale. During these years, radio-collared females in mixed-sex groups dispersed from different locations into different regions during the same season, although events may have been separated in time by several weeks.

Group size and stability. Dispersing female muskoxen did not disperse as solitary individuals but were always in mixed-sex groups. The average size of mixed-sex groups with which dispersing females were associated was smaller ($t_{12} = 2.74$, $P = 0.011$) after dispersal events took place (Table 10). Eleven of 13 mixed-sex groups declined in size, 6 groups lost ≥ 1 radio-collared animals and 3 groups gained other marked animals between the onset and end of dispersal. Group size was not different before and after the 5 outward ($t_7 = 0.04$, $P = 0.97$) and return ($t_7 = 1.02$, $P = 0.34$) transitory events (Table 10).

Mean group size in regions first occupied did not differ by year in 1982-1995 ($F_{13, 661} = 1.24$, $P = 0.24$). But before the first large pulse of dispersal in 1986-87, size of mixed-sex groups showed an increasing trend from 1982 to 1986 and a similar trend occurred between 1988 and 1993 before animals dispersed in 1994 (Fig. 15). Mean group size was not different ($t_{14} = 0.74$, $P = 0.89$) and followed similar patterns between regions first occupied and regions occupied later (Fig. 15).

Age and reproductive status. Radio-collared females in mixed-sex groups that were involved in dispersal or transitory events ranged in age from 3 to 10 years. The average birth year estimated for these females was not significantly different from that of nondispersing females ($t_{25} = 1.14$, $P = 0.26$). Reproductive indices calculated for dispersing and exploratory females were not different ($t_{25} = 0.65$, $P = 0.52$) from

those calculated for philopatric females (Table 11). Reproductive indices were based on total reproductive effort, both before and after dispersal. Seven of 11 dispersing females had calves after dispersing, one did not calve, and the reproductive status of 3 individuals was not determined, but sample sizes were too small to compare reproduction by radio-marked females before and after dispersal.

Calf production and young animal survival. Calf production declined from 1977 to 1997 ($b = -3.3$, $r^2 = 0.78$, $P < 0.001$) in regions first occupied and was lower ($\bar{x} = 44$) than calf production in regions occupied later ($\bar{x} = 56$) in 1986-97 ($t = 3.53$, $P = 0.005$). But both areas showed the same annual trends in 8 of 11 years (Fig. 16). Survival of young in regions first occupied did not decline between 1984 and 1995 (calf survival: $b = -0.01$, $r^2 = 0.01$, $P = 0.72$; yearling survival: $b = -0.004$, $r^2 = 0.006$, $P = 0.82$). Annual variability in calf and yearling survival were correlated ($r = 0.81$, $P = 0.002$) and followed the same annual trends as calf production in 9 of 10 years from 1985 to 1995 (Fig. 3). Annual variability in survival was correlated with snow depth in winter (Chapter 1).

DISCUSSION

Attributes associated with dispersal events and range expansion

Initiation of most dispersal events between late June and September indicated that females in mixed-sex groups dispersed primarily in mid-summer or late summer. Muskoxen moved more during summer to take advantage of the availability of green forage in a wide variety of habitats (Chapter 2). The energetic costs of moving through snow and the limited availability of forage in winter may discourage long-distance movements in that season. The proximity of long movements to the peak of the growing season suggests that seasonal, transitory or dispersal events were related to the acquisition of forage during the short arctic growing season. Alternatively, animals

may not need to move much in summer because of the relative abundance of forage and mid-summer movements may be related to the presence of insects, weather conditions, or predators. Dispersal also occurred immediately before and during the mating season (rut) when social interactions were high and when female muskoxen made rapid gains in weight (Adamczewski et al. 1992).

Juxtaposition of dispersal pulses in years of short cold summers followed by winters of deep snow indicate that weather conditions play an important role in distribution of this muskox population. Plant production is lower in cold summers when the length of the growing season is reduced (Chapin 1983). Female muskoxen may make longer movements and traverse over larger areas to insure adequate intake of forage during these cold short summers. In years of deep snow, less forage is accessible, and muskoxen use more energy cratering through snow and moving between forage patches. Short cold summers and winters with deep snow can result from atmospheric conditions affecting weather on a global scale such as occurred in 1991-92 after the eruption of Mount Pinatubo in the Philippines on 15 June 1991.

Dispersal destinations may be influenced by the presence of conspecifics. On the Seward Peninsula, mixed-sex groups dispersed into regions first occupied by males (Smith 1989) and, in northeastern Alaska, this pattern also prevailed as mixed-sex groups dispersed into drainages that had been occupied by bull groups several years earlier (P. E. Reynolds, unpubl. data). Like many mammals, male muskoxen disperse more frequently than do females as a strategy to increase their probability of breeding (Smith 1989). In this study, bull groups or solitary bulls were observed south of the Brooks Range mountains hundreds of kilometers beyond the distribution of mixed-sex groups, and 3 to 4-year-old radio-collared males moved into previously unoccupied regions or disappeared from the study area (P. E. Reynolds, unpubl. data). This suggests that many male muskoxen disperse from natal areas as they approach sexual maturity, but are still too young to win dominance fights. Smith (1989) reported that

younger and older males were more likely to disperse than bulls 6-9 years-of-age. In species with polygynous mating systems, males that are unlikely to successfully compete for mates are the most likely component of the population to emigrate (Brandt 1992).

The rapid long-distance movements (17-22 km/day) associated with the onset of dispersal events by satellite-collared females were unusual because female muskoxen are energetically conservative animals (Klein 1992). Daily rates of movement calculated from locations of satellite collared females averaged only 3.7 km/d in July, when maximum rates for the year were recorded (Chapter 2. Table 5). These rapid movements suggest that at least some dispersal events are triggered by disruptive local conditions such as predation or social stress during the mating season.

High rates of productivity and survival during the first decade after release of muskoxen in regions first occupied were attributed to the abundance of high quality forage (Jingfors and Klein 1982) that likely decreased as animal densities increased and plant communities responded to grazing pressure. In addition to changes in habitat, and annual variability due to weather, increased predation also likely affected calf production over time, either directly from neonates killed by predators, or indirectly via deaths that occurred when young calves were left behind by muskoxen fleeing from predators (P.E. Reynolds, unpubl. data). For several years after muskoxen were released, predation rates were low presumably because predators had no experience with killing muskoxen and muskox densities were low (Chapter 1). Also wolves were likely at low densities on the coastal plain of the Arctic NWR in winter because few other large ungulates were present year-round until the muskox population became established.

The lower rates of calf production observed in regions first occupied, compared with regions occupied later, likely reflected differences in habitat and levels of predation. The ungrazed habitats in regions occupied later by mixed-sex groups

probably provided better forage than regions occupied for the first 15 years after the release of muskoxen in northeastern Alaska. High rates of calf production in regions occupied later also may be beginning to moderate in response to changes in habitat and increased predation.

Genetically based tendencies to disperse or remain in home ranges have been the subject of speculation for small mammals (Gaines and McClenaghan 1980). Dispersing female muskoxen made more seasonal shifts outside home ranges than did nondispersing females, suggesting that some individuals had a greater propensity for making long movements that resulted in seasonal shifts and dispersal. Female muskoxen dispersed in groups, not as individuals, and the role of leadership in directing the movements of mixed-sex groups was not addressed in this study, the importance of individual variation in the process of dispersal could not be determined.

Dispersal models

Diffusion dispersal. Dispersal of muskoxen in northeastern Alaska was not a process of simple diffusion as mixed-sex groups did not continuously disperse in all directions during all seasons (Table 12). The diffusion model was not supported by combining probabilities (Sokal and Rohlf 1981, p. 780) from tests of significance ($-2(\sum \ln P) = 1.308$, $\chi^2_{0.01(6)} = 16.812$). The pulses of dispersal from regions first occupied as well as the seasonal nature and the occurrence of multiple events in one year showed that dispersal of mixed-sex groups was a periodic process occurring on a regional scale. Although several studies have proposed that animals disperse in a random direction into the nearest vacant habitat (Murray 1967), the availability of forage in habitats used by muskoxen varies annually due to the length and temperature of the summer growing season and the depth of snow in winter. This annual variability contributed to the pulsed pattern of dispersal observed in these large herbivores.

Weather effects: density independent dispersal. Predictions about the relationship between weather conditions and the dispersal of mixed-sex groups were

supported by observations of dispersal (Table 12). The occurrence of pulses of dispersal during short cold summers followed by winters with deep snow indicate that annually changing conditions in the environment influenced the distribution of muskoxen. The relationship between snow depth and animal survival emphasizes the importance of weather on animal species living in the Arctic. The initiation of dispersal events in mid- to late summer corresponded to the seasonal availability of green forage needed for lactation and weight gain. The similar annual trends in mean group size and in calf production between regions first occupied and regions occupied later suggest a relationship with conditions, like weather, that occur on a large scale. Weather events could influence animal distribution either directly by making forage inaccessible or energetically costly to obtain (e.g. through deep snow), or indirectly through factors that decrease plant production. Weather is a more important factor in extreme environments like the Arctic than in more moderate climates.

Habitat change: density dependent saturation dispersal. Declines in calf production in regions first occupied and rapid increase in population abundance followed by decline and stabilization (Ch. 1 Fig. 2) in regions first occupied indicated that density-dependent factors affecting habitat were responsible for some of the observed changes in the distribution of mixed-sex groups (Table 12). The first large pulse of dispersal in 1986-87 occurred when numbers of muskoxen in regions first occupied reached a maximum, indicating that this initial pulse was related to animal density. Lower productivity in regions first occupied compared with regions occupied later, where grazing by muskoxen had occurred for fewer years, also indicated a relationship between density and habitat. However, similar trends in the annual variability of calf production in both regions first occupied and occupied later, and the high annual variability in calf production suggested that weather also played a major role in calf production.

The lack of a declining trend in survivorship of calves and yearlings over time in the years before the first pulse of dispersal suggested that although changes in habitat likely occurred, habitats were not severely depleted by high population densities (Table 12). Group size did not decline before the first pulse of dispersal. The habitat change model was not supported by combining probabilities (Sokal and Rohlf 1981, p. 780) from tests of significance ($-2(\sum \ln P) = 12.123$, $X^2_{0.01(4)} = 13.277$).

Social factors: density dependent pre-saturation dispersal . An increasing trend in mean group size that occurred before the first large pulse of dispersal and then became relatively stable indicated that an upper threshold of social saturation may have been reached. The same trend with a similar magnitude also occurred in regions occupied later. The habitat change model was supported by combining probabilities (Sokal and Rohlf 1981, p. 780) from tests of significance ($-2(\sum \ln P) = 19.827$, $X^2_{0.01(4)} = 13.277$).

Group living is advantageous for predator detection and feeding efficiency (Heard 1992), but can result in intraspecific competition for forage and other life-sustaining requirements (Lott and Minta 1983) or for mates. In highly gregarious herbivores like muskoxen, that have evolved an effective group defense against predators, a balance between benefits and costs to individuals lies within some range of group size. Group size did not follow a negative exponential distribution (Lott and Minta 1983) suggesting that groups are of adaptive value and do not form via a random assortment of individuals.

Most mixed-sex groups fractured into smaller units before or during the process of dispersal. This instability suggests a relationship between social behavior and dispersal. Also, most dispersal took place just prior to or during rut in August and September. On the average, mixed-sex groups of muskoxen were larger in winter and smaller in summer, reaching a minimum in August during the peak of rut, a seasonal decline likely associated with the polygynous mating system (Reynolds 1992). Changes

in group size also may be an anti-predation strategy (Heard 1993), or may reflect increases in the percentage of young animals in a growing population. Predator attacks could trigger movements that result in dispersal. Muskoxen in Canada moved > 50 km in response to brown bears killing calves (Clarkson and Liepins 1995). Instability in mixed-sex groups of muskoxen could occur during predator attacks if muskoxen running in panic flight split into smaller groups that may move in different directions and become separated.

The initiation of most dispersal events between late June and September indicates a relationship with the mating season. Bulls wintering together in groups begin to disband by June and individual bulls show evidence of aggressive behavior associated with mating by July. I hypothesize that breeding bulls may try to sequester females in mixed-sex groups from other animals by moving them to regions of lower density, including regions into which they dispersed some years earlier. Alternately, dominant females may try to eject subordinate females if food resources are limited. Pre-saturation dispersal has been documented in small mammals where social factors motivate dispersal long before resources become limiting. Behavior-related causes include social subordination resulting from density-dependent aggression, genetic differences of individuals within the population, and social cohesiveness (Gaines and McClenaghan, 1980).

Summary and conclusions

The expansion of the muskox population in northeastern Alaska that occurred when mixed-sex groups began to disperse from regions first occupied was a complex process likely involving several interacting factors (Fig. 13). Female muskoxen in mixed-sex groups dispersed infrequently and had a high fidelity to range. Dispersal of mixed-sex groups was not simple diffusion, but occurred as a series of periodic pulses in short cold summers followed by winters of deep snow. Dispersing mixed-sex groups moved along an east-west axis likely funneled by environmental features of

terrain and land cover. Population density was a factor, particularly in the first large pulse of dispersal. Both social factors and changes in habitat, indicated by declining trends in calf production, played a role in density-dependent dispersal. Because of the extreme conditions of the arctic environment and the annual variability in snow depth and summer temperatures, weather conditions also influenced the distribution of mixed-sex groups and their dispersal into new ranges in northeastern Alaska.

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Table 8. Predictions used to evaluate models (in bold capital letters) that explain the process of dispersal of mixed-sex groups in an expanding population of muskoxen in northeastern Alaska, 1986-95.

Attributes	Predictions	
	Accept model	Reject model
DIFFUSION		
Abundance + size of use areas	Correlated	Not correlated
Dispersal interval	Continuous	Irregular pulses
Dispersal direction	All directions	Along axis
Season of dispersal	All seasons	In specific seasons
WEATHER EFFECTS: Density independent dispersal		
Dispersal and weather events	Correlated	Not correlated
Season of dispersal	Late winter or mid-summer	All seasons
Magnitude of dispersal	Regional scale	Local scale
HABITAT CHANGE OVER TIME: Density dependent saturation dispersal		
Pre-dispersal calf production	Declining trend	No decline
Pre-dispersal survivorship	Declining trend	No decline
Pre-dispersal group size	Declining trend	No decline
SOCIAL FACTORS: Density dependent pre-saturation dispersal		
Pre-dispersal group size	Increasing trend	Not increasing
Dispersing group stability	Change in group size	No change
Season of dispersal	Rut	All seasons

Table 9. Dates, distances moved, and minimum rates of movement associated with dispersal events made by satellite-collared female muskoxen in northeastern Alaska.

Muskox number	Dates of long movement that begin dispersal event		Distance and direction	Rate of movement
	Begin	End		
64	July 24 1989	July 27 1989	51 km west	17 km/day
73	July 13 1991	July 15, 1991	43 km west	22 km/day
73	July 8 1992	July 10, 1992	38 km west	19 km/day

Table 10. Change in the size and stability of mixed-sex groups of muskoxen with which radio-collared females were associated before and after transitory ($n = 5$) and dispersal ($n = 13$) events occurred in northeastern Alaska, 1986-95.

	Size of mixed-sex groups		Groups with radio-collared animals leaving or joining	
	\bar{x}	SD	Number of groups	Percentage of groups
Before transitory events began	20.2	16.5		
After transitory events ended	20.6	12.5	2	0.40
Before dispersal events began	25.4	11.0		
After dispersal events ended	14.9	8.3*	10	0.76

*group size was significantly less after event ($t_{13} = 2.74$, $P < 0.001$).

Table 11. Estimated minimum birth year and reproductive indices of dispersing and non-dispersing female muskoxen in northeastern Alaska. Values were not significantly different (birth year: $t_{25} = 1.14$, $P = 0.26$; reproductive index: $t_{25} = -0.65$ $P = 0.52$).

Type of female	n	Birth year		Calves per year	
		\bar{x}	Range	\bar{x}	SD
Dispersers ^a	13	1983	1968-88	0.51	0.21
Nondispersers	14	1981	1978-88	0.56	0.22

^afemale muskoxen in mixed-sex groups that made movements resulting in transitory or dispersal events.

Table 12. Observed attributes associated with dispersal of mixed-sex groups of muskoxen in northeastern Alaska compared with predictions that were used to evaluate dispersal models.

Attribute	Predicted	Observed	<i>P</i>
DIFFUSION			
Abundance + size of use area	Correlated	Not correlated	>0.51
Dispersal interval	Continuous	Periodic pulses	
Dispersal direction	All directions	East-west axis	>0.95
Season of dispersal	All seasons	Midsummer+rut	>0.95
WEATHER EFFECTS: Density independent dispersal			
Dispersal + weather events	Correlated	Correlated	0.0287
Season of dispersal	Winter/summer	Mid summer+rut	
Magnitude of dispersal	Regional scale	Regional scale	
HABITAT CHANGE OVER TIME: Density dependent saturation dispersal			
Pre-dispersal calf production	Declining trend	Declining trend	0.003
Pre-dispersal survivorship	Declining trend	No trend	0.777
Pre-dispersal group size	Declining trend	Increasing trend	
SOCIAL FACTORS: Density dependent pre-saturation dispersal			
Pre-dispersal group size	Increasing trend	Increasing trend	0.055
Dispersing group stability	Change in size	Change in size	<0.001
Season of dispersal	Rut	Mid summer+rut	

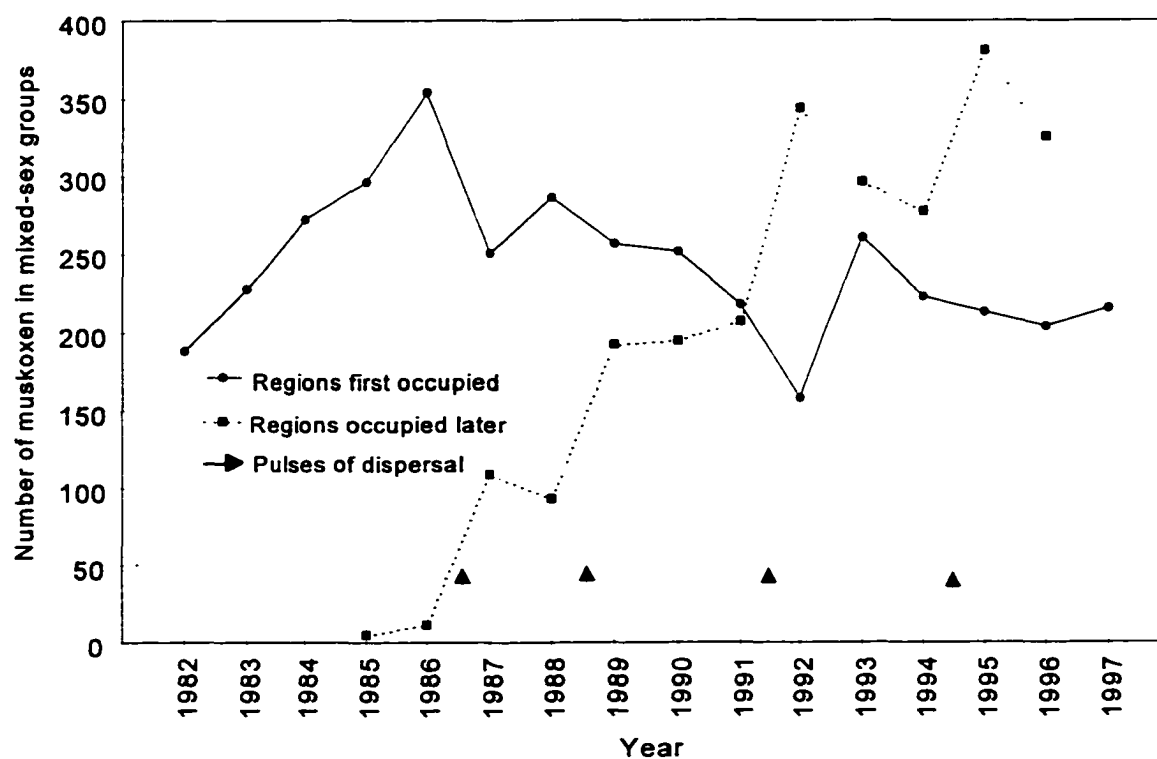


Fig. 9. Shifts in numbers of muskoxen associated with mixed-sex groups between regions first occupied and regions occupied later in northeastern Alaska. These shifts indicated when pulses of dispersal occurred.

Year	West of study area	Western regions occupied later	Regions first occupied	Eastern regions occupied later	East of study area
1982					
1983					
1984					
1985					
1986		<----- <-----	----- -----		
1987		<-----	-----		
1988		<-----	----- -----	-----> ----->----->	
1989		<----- <-----	----- ----- ----->		
1990				-----	----->
1991		<-----	-----		
1992		<-----			
1993					
1994	<-----	-----			
1995					

Fig. 10. Year, location, and direction of dispersal events made by radio-collared females in mixed-sex groups of muskoxen in northeastern Alaska.

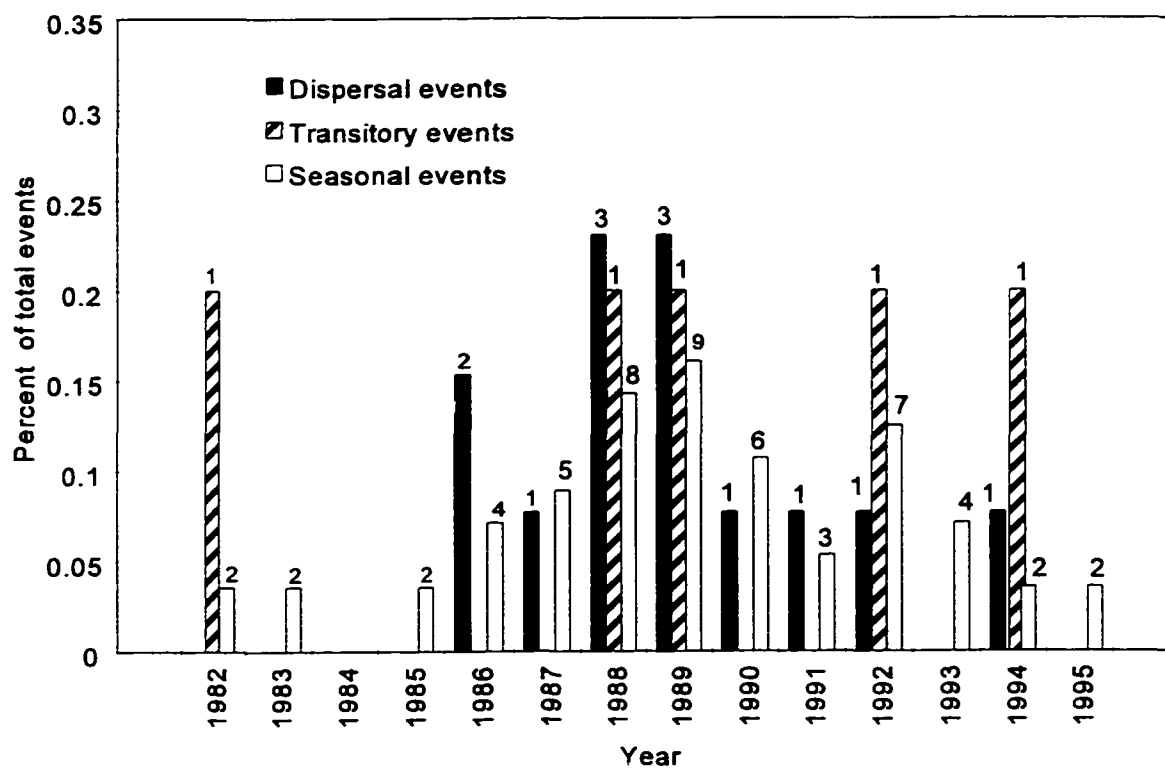


Fig. 11. Years in which in which radio-collared females in mixed-sex groups of muskoxen initiated seasonal, transitory and dispersal events in northeastern Alaska. Sample sizes are provided above bars.

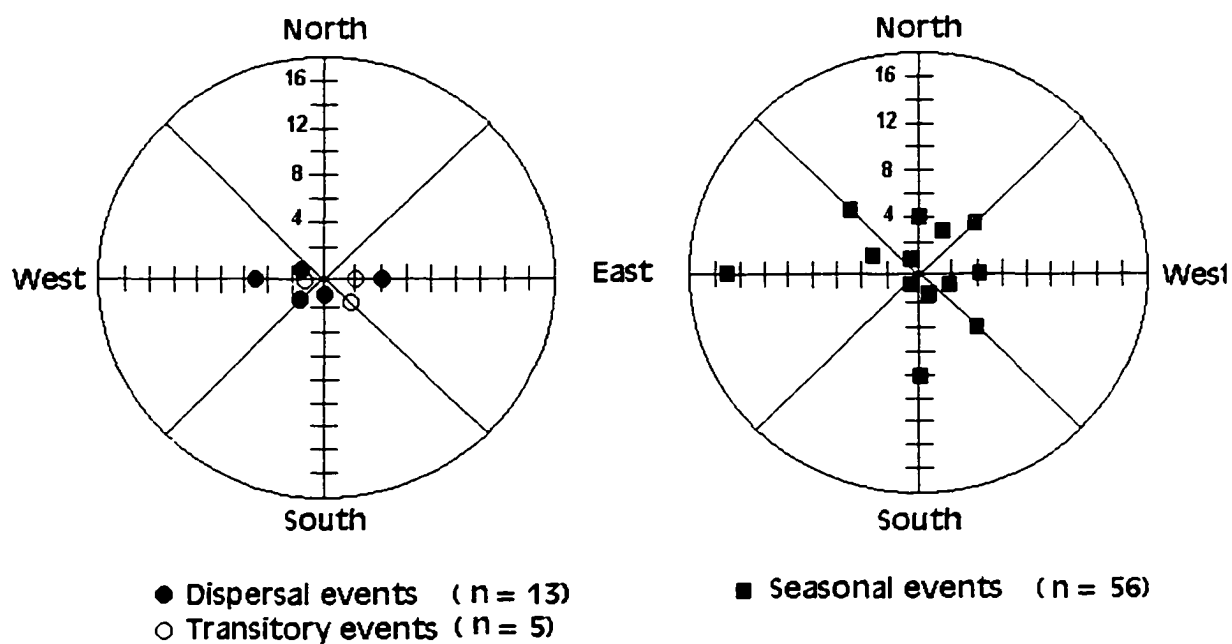


Fig. 12. Directions moved by radio-collared female muskoxen in mixed-sex groups during outward movements associated with seasonal, transitory and dispersal events in northeastern Alaska, 1982-95.

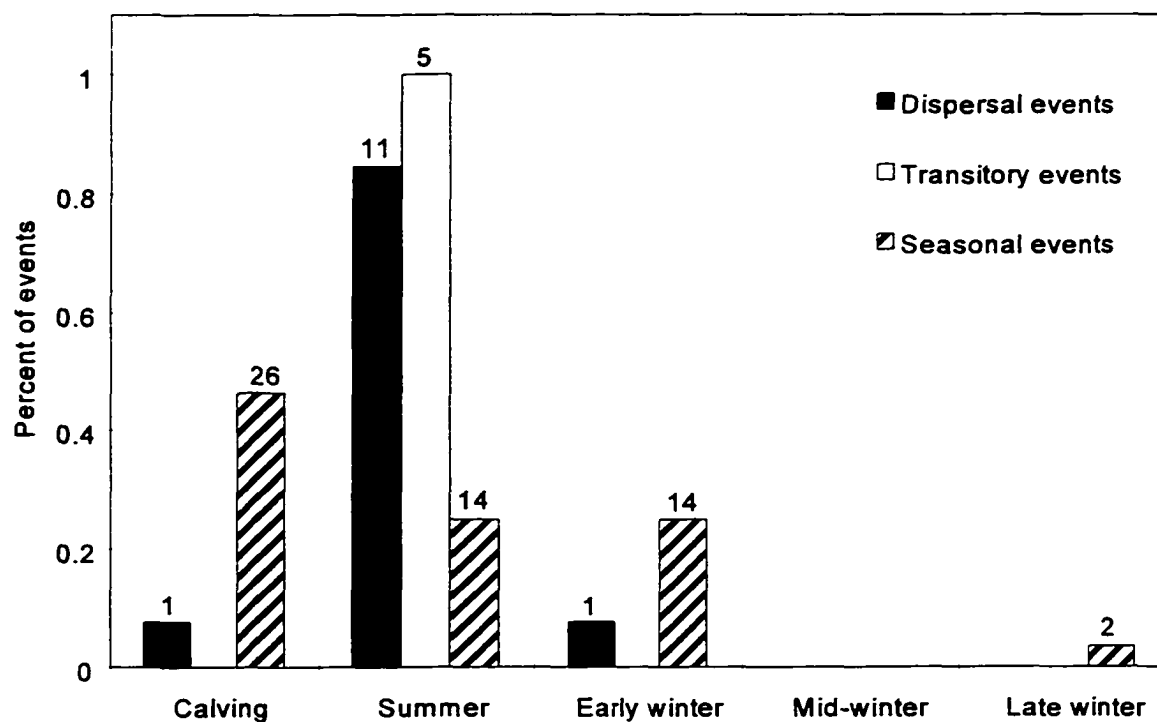


Fig. 13. Seasons when radio-collared female muskoxen in mixed-sex groups made outward movements associated with seasonal shifts in distribution, transitory or temporary dispersal and permanent dispersal into new home ranges in northeastern Alaska, 1982-95. Summer included the mating season (rut) in August and mid-September. Sample sizes are provided above bars.

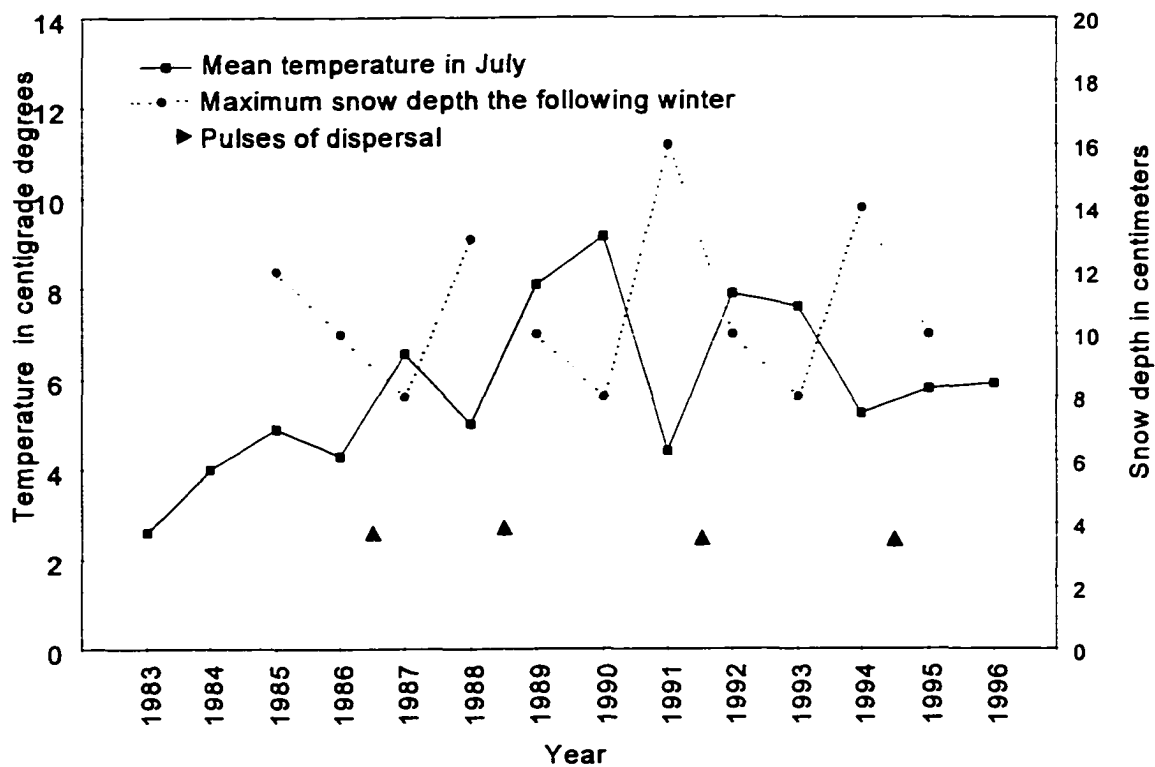


Fig. 14. Relationship between pulses of dispersal of mixed-sex groups of muskoxen and weather conditions in northeastern Alaska. Mean air temperature (C°) in July was measured at Barter Island (National Oceanic and Atmospheric Administration climatological data) and maximum snow depth the following winter was measured at an inland site in north-central Alaska (Kane 1997).

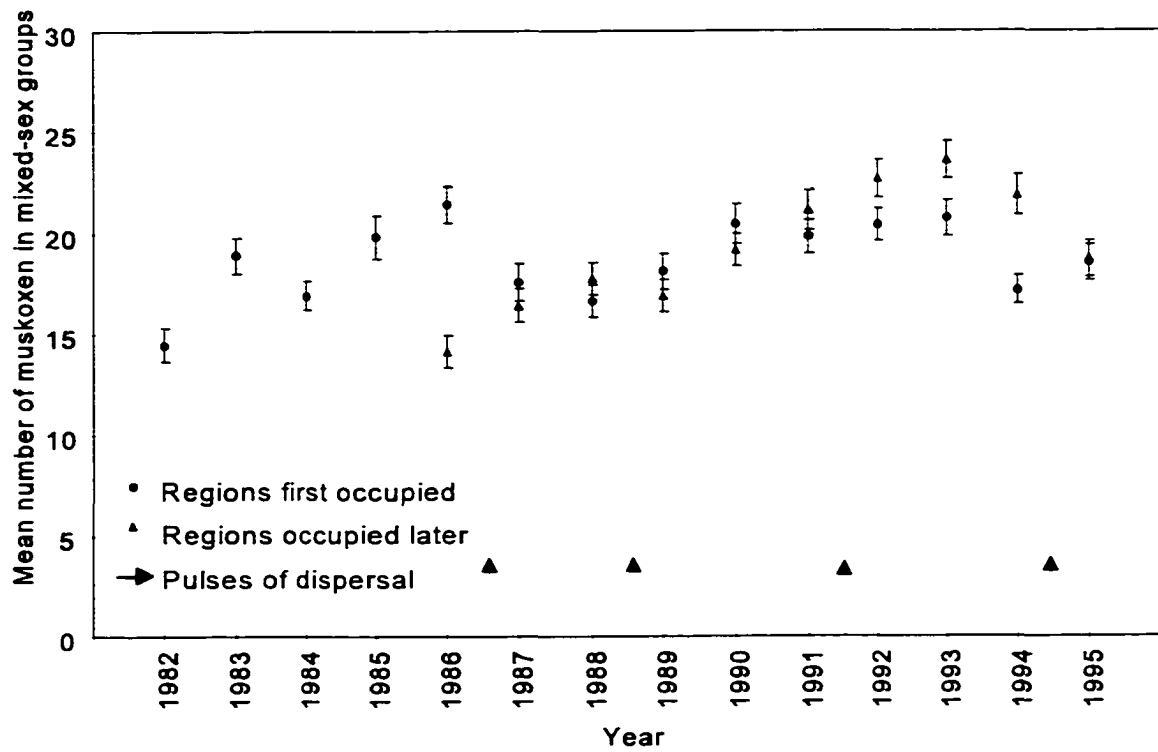


Fig. 15. Change in size of mixed-sex groups of muskoxen in regions first occupied and regions occupied later in northeastern Alaska, 1982-95. Vertical bars are 1 standard error.

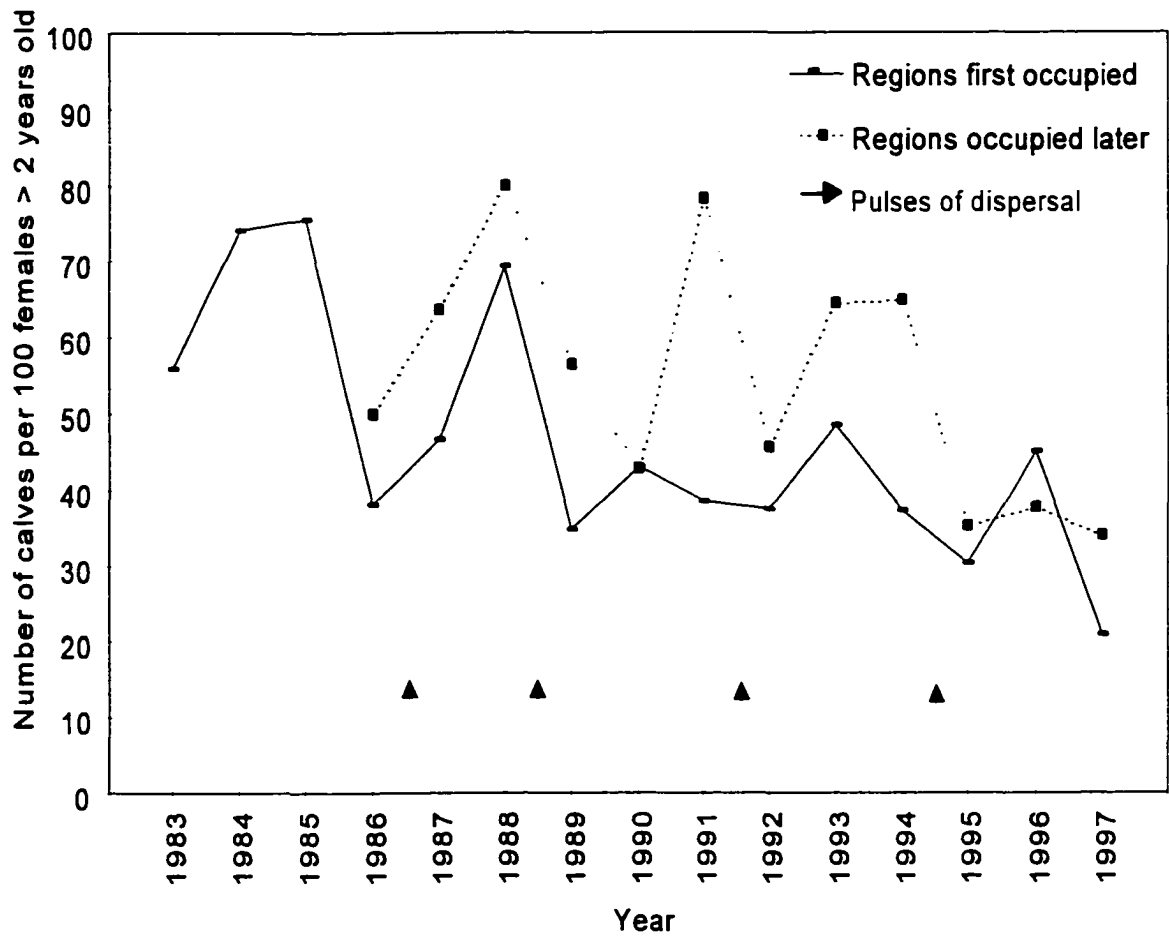


Fig. 16. Calf production in regions first occupied and regions occupied later by mixed-sex groups of muskoxen in northeastern Alaska, 1983-97.

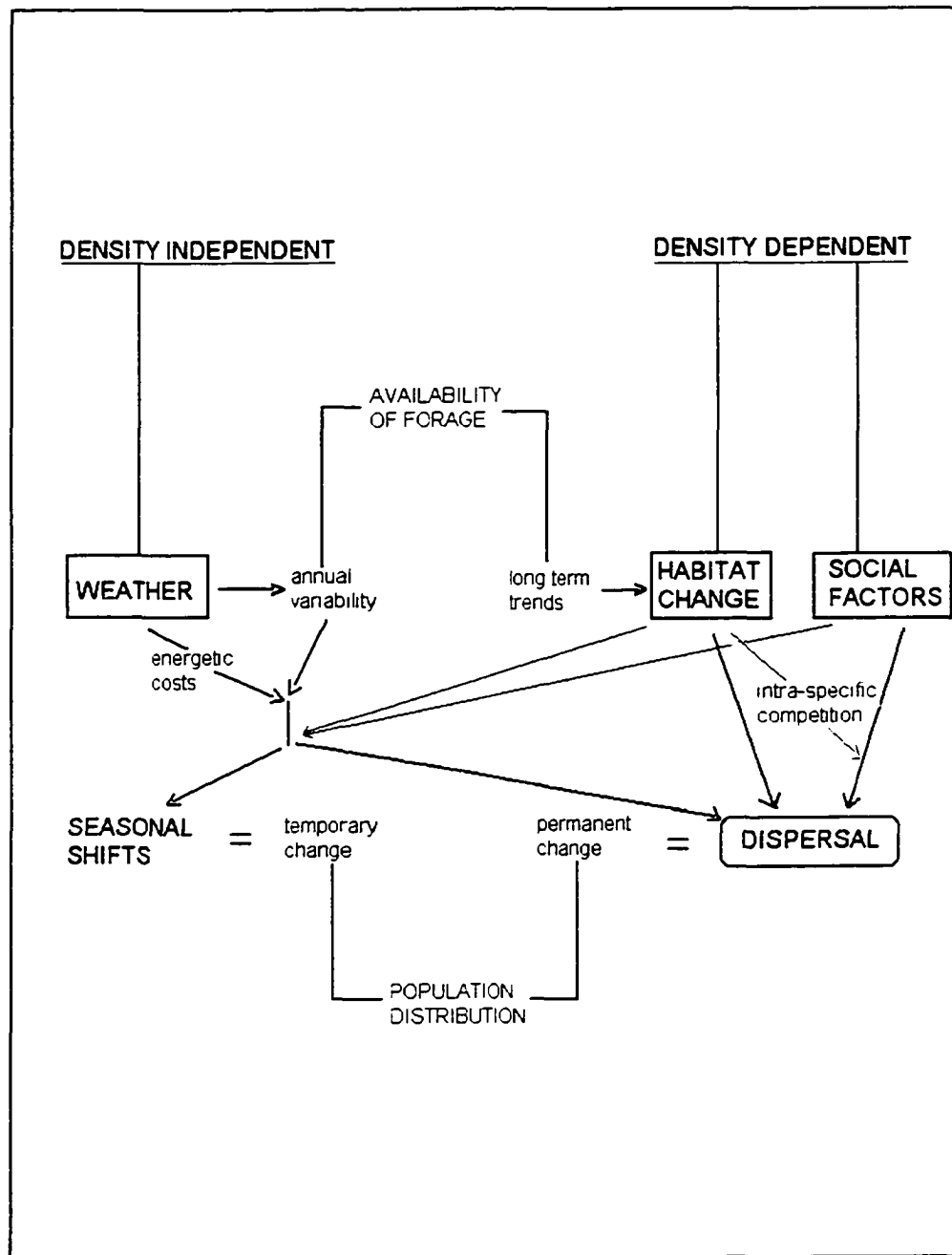


Fig. 17. Relationship between density dependent and independent factors that may have resulted in shifts in distribution and dispersal of mixed-sex groups of muskoxen in northeastern Alaska, 1986-1995.

SYNOPSIS AND CONCLUSIONS

The successful return of muskoxen to northeastern Alaska after an absence of many decades was the result of several factors that affected rates of population growth and changes in population distribution. The presence of unexploited habitats suitable for muskoxen in the Arctic NWR and a lack of predation contributed to high rates of calf production and animal survival during the decade from 1976 to 1986. Subsequent declines in calf production and stabilization of muskox abundance in regions first occupied were likely due to changes in habitat as animal densities increased. Predation by brown bears and wolves also increased and likely influenced the downward trend in calf production and population stabilization. Rates of survival of calves and yearlings did not decline over time. Annual variability in calf production and survival of young animals was related to snow depth: in years of deep snow, both calf production and rates of survival were low. Survival was high in years of low snow. Dispersal of mixed-sex groups also contributed to the stabilization of numbers of muskoxen in regions first occupied.

Muskoxen reestablished into formerly occupied range in northeastern Alaska live year-round on the coastal plain of the Arctic NWR. Females in mixed-sex groups have a high fidelity to geographic regions. These animals are subjected to seasonal variations in the quality and availability of forage that influence seasonal distribution, rates of movement, activity patterns and habitat use. During the short weeks of the summer season, muskoxen need to replace body weight lost during the previous winter and during pregnancy and lactation. Muskox strategy during the short summer is to maximize energy intake, which is accomplished by foraging in diverse habitats. Increased movements, occupation of larger areas during the course of the summer, and the use of most available habitats are means by which this energy-maximizing strategy is accomplished.

During the long winter months, when climatic conditions are severe and snow limits accessibility to forage and is a barrier to efficient movements between forage patches, muskoxen have a strategy of energy conservation. Reducing movements and activity, decreasing the size of use areas, and using only a few habitat types are methods to conserve energy. Because muskoxen give birth in April and May when weather conditions in northeastern Alaska are still severe, pregnant females must be energetically conservative throughout the winter to maintain body reserves for lactation during the 4 to 6 weeks until green forage is available.

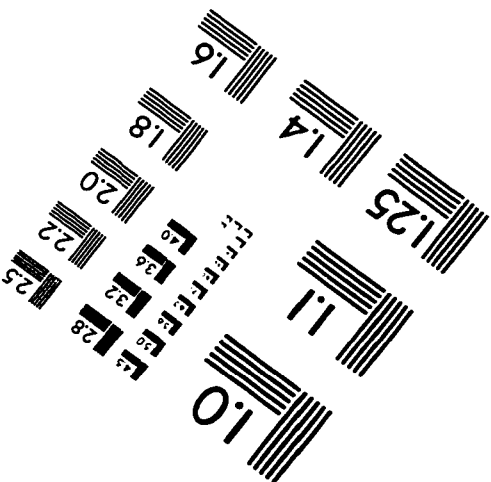
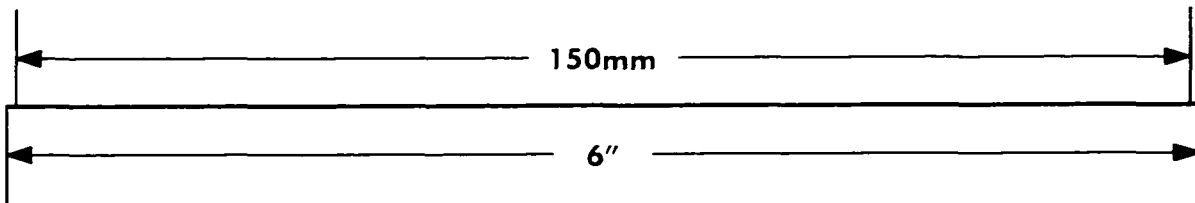
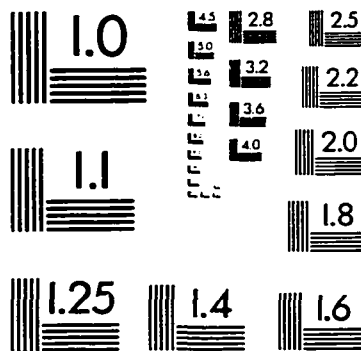
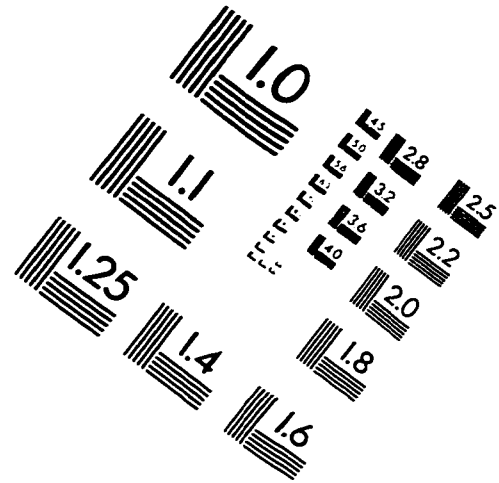
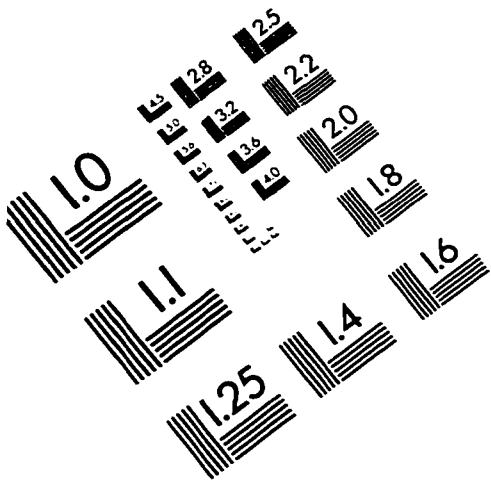
In this expanding population of muskoxen, dispersal of mixed-sex groups was a significant component in the stabilization of animal numbers and the mechanism by which muskoxen moved into unoccupied habitats. Dispersal was not a process of simple diffusion, but occurred in periodic pulses that were related to weather events and population density. Changes in habitat likely took place as grazing pressure increased and plants adjusted to higher densities of animals, but social factors were also important in the dispersal of mixed-sex groups.

Weather conditions played a major role in the ecology of this arctic-adapted ungulate. The length and coolness of the summer season influences plant growth which in turn affects the amount of gain in body mass. Body reserves put on during and after the short summer growing season affect survival the following winter, and reproduction in subsequent years. Shifts in distribution during short cold summers that result in dispersal could be part of the energy-maximizing strategy used by muskoxen in summer.

In northeastern Alaska, snow is present for most of the year (8-9 months of the year). Deep snow is energetically costly for muskoxen to move through and to dig through for food and can limit the availability of forage for many months. Annual variability in snow depth influences survivorship, and to a lesser extent, calf production, as well as seasonal distribution of animals, and shifts in distribution over time. Muskoxen are adapted for living under the arctic conditions of extremes in day length,

severe cold, and low quality and quantity of vegetation throughout most of the year. But snow depth in northern Alaska, especially when interacting with other variables, may be a limiting factor with respect to population size and distribution.

IMAGE EVALUATION TEST TARGET (QA-3)



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